THE INFLUENCE OF WATER VELOCITY AND DEPTH ON PREY DETECTION AND CAPTURE BY JUVENILE COHO SALMON AND STEELHEAD: IMPLICATIONS FOR HABITAT SELECTION AND SEGREGATION

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By

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ABSTRACT

I studied the effects of water velocity and depth on drift-foraging by juvenile coho salmon and steelhead to assess how these influence their reported habitat segregation into pools and riffles, respectively. I used three-dimensional video analysis of stream-tank foraging experiments to test how velocity and depth influence prey capture probabilities, and the geometry and dynamics of prey detection and capture. I used the experimental results to develop net energy intake models to predict optimal foraging velocities for coho and steelhead.

Prey capture probabilities for both coho and steelhead declined from ~65% to 10% with an increase in velocity from 0.29 to 0.61 $m \cdot sec^{-1}$, with little difference between the species. Capture maneuver characteristics were similar for both species, including reduced prey detection distance and capture probabilities within the capture area, constant prey interception speed, and increasing return speed. I conclude that faster velocity reduces prey capture success by coho and steelhead, but that differences in capture abilities are not responsible for habitat segregation.

Prey capture probabilities for both species were constant at ~ 40% at depths from 0.15 to 0.60 m, with little difference between the species. Capture maneuver characteristics were similar for both species, including increased prey detection distance and interception speed, and constant return speed. I predict that prey capture rate increases proportionally to water depth for coho and steelhead, but that differences in capture probabilities are not responsible for habitat segregation.

I used the experimental results to develop net energy intake models that predicted optimum foraging velocities of 0.29 m · s^{-1} for coho and 0.30 m · s^{-1} steelhead. Modeled 10% and 25% increases in swimming costs for coho reduced optimum velocity by 0 and 0.01 m · s^{-1}, respectively. These results, coupled with those from the depth experiments, suggest that habitat segregation may be due to factors other than short-term foraging considerations. I propose that these are largely selective mechanisms such as size-based habitat selection, differences in growth trajectories, or prey specialization. I do not discount the possibility that interactive mechanisms are also important, especially at periods of high fish density or limited prey availability.

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GENERAL INTRODUCTION

"When I said that you stimulated me I meant, to be frank, that in noting your fallacies I was occasionally guided towards the truth" Sherlock Holmes to Dr. Watson, *in* The Hound of the Baskervilles by Sir Arthur Conan Doyle

Coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss irideus*) are distributed around the Pacific Rim from central California to south-central Alaska, and into parts of Asia. (Behnke 1992, Groot and Margolis 1991). Coho are semelparous fall spawners, and steelhead are iteroparous spring spawners (Behnke 1992, Groot and Margolis 1991). Juveniles of both species rear in freshwater for one or more summers before migrating to ocean environments, and are often found in sympatry where their distributions overlap (Hartman 1965, Allee 1974, Bugert et al. 1991). Coho fry emerge earlier in the year than do steelhead, and they typically have a size advantage during their first summer in streams (age 0+) (Hartman 1965). Steelhead grow more quickly than do coho, however, so by the end of this first growing season fish of both species are often the same size (Hartman 1965, Fraser 1969). In the southern portions of their respective ranges, most coho emigrate as smolts the following spring (age I+), thus avoiding size overlap and potential competition with steelhead during their second summer (Hartman 1965, Allee 1974). In these systems steelhead typically smolt the following year as age II+. In Southeast Alaska both species usually spend an extra summer in streams, and size overlap occurs among age I+ coho and steelhead before the coho emigrate the following year as age II+ (Lohr and Byrant 1999, Halupka et al. 2000).

Although they often occur within the same stream reach, coho and steelhead have been documented to segregate microhabitat, with coho using slower, deeper pools and steelhead using faster, shallower riffles (Hartman 1965, Allee 1974, Bisson et al. 1988, Bugert et al. 1991). A similar pattern of pool/riffle segregation has also been reported for other sympatric stream fish, both salmonid (see Hearn 1987), and non-salmonid (Gorman 1988), and it has been proposed that habitat complexity is a driving force behind species richness of stream fishes (Gorman and Karr 1978, Young 2001).

Explanations for habitat segregation in coho and steelhead have included both of Nilsson's (1967) proposed mechanisms for species segregation: 1) interactive segregation, whereby one species displaces the other from a preferred habitat (Hartman 1965, Young 2004), and 2) selective segregation, whereby the species select their respective habitats based on differential abilities to forage there (Fraser 1969, Allee 1974, Bugert and Bjornn 1991). Hartman (1965) documented the distribution of age 0+ coho and steelhead in the Salmon River, British Columbia, and he conducted laboratory experiments to identify the mechanism for segregation. He found that in summer, coho were more aggressive in pools, and steelhead in riffles, and he proposed that these behavioral differences facilitated segregation. Allee (1974) observed that in natural streams, however, interspecific interactions between coho and steelhead were relatively rare, and he concluded that segregation was largely selective and size-based. In other laboratory studies, Fraser (1969) and Bugert and Bjornn (1991) have also favored the selective hypothesis, whereas Young (2004) has documented a size-based competitive advantage for coho. Observational-intensive field studies of coho and steelhead in

sympatry are lacking, however, so the relative importance of interactive vs. selective segregation is unknown.

Ecological theory suggests that the niches of two sympatric species cannot entirely overlap (Zaret and Rand 1971, Schoener 1974, Abrams 1983), and habitat segregation in sympatric stream salmonids is thought to be based in part on species-specific differences in foraging abilities (Allee 1981, Bisson et al. 1988, Bremset and Berg 1999, Young 2001). Bisson et al. (1988) proposed that the more laterally-compressed body and taller median fins of coho allow them to forage better in slower water, whereas the more cylindrical body and shorter median fins of steelhead facilitates foraging in faster water. They suggested that coho are better at rapid acceleration and turning, which facilitates foraging on patchy prey in slower water, whereas steelhead are better at foraging in faster water because of reduced hydrodynamic drag. Although morphology-based differences in foraging efficiency have been demonstrated to facilitate habitat segregation by pond-dwelling sunfish (Werner and Hall 1979), the relative abilities of coho and steelhead to forage in slow vs. fast water have not been addressed. In Chapter One I present the results of experiments designed to assess the effects of water velocity on the foraging abilities of coho and steelhead.

Within microhabitats, coho have been shown to forage nearer the surface, and steelhead nearer the substrate (Fraser 1969, Johnston 1970, Allee 1981). Both species have also been shown to segregate along the water depth axis with other species of salmonids (Bravender and Shirvell 1990, Dolloff and Reeves 1990) or intraspecifically by size (Nielsen 1992, Harvey and Nakamoto 1997). Water depth is an important niche

axis for segregation in other species of stream fish as well, both salmonid (Gibson and Power 1975, Bagliniere and Arribe-Moutounet 1985, Heggenes et al. 1999), and non-salmonid (Greenberg 1991, Reyjol et al. 2001, Jowett 2002, Hesthagen et al. 2004). Although depth is a commonly-measured feature of stream habitat (Bovee 1978), there has been virtually no research on the underlying reasons why fish select certain depths or why depth-based segregation is common in stream fish. In Chapter Two I present the results of experiments on the effects of water depth on the foraging abilities of coho and steelhead.

Animals are thought to select habitat based in part on the relative costs and benefits of foraging there (MacArthur and Pianka 1966, Stephens and Krebs 1986). For drift-feeding salmonids, the metabolic cost of foraging against a current is balanced against the benefit of more prey encounters in faster water (Everest and Chapman 1972, Wankowski 1981). The velocity at which a fish can maximize its net energy intake (NEI) rate is determined by the relative magnitude of its costs vs. benefits; it follows that two co-evolved sympatric species such as coho and steelhead might reduce niche overlap by maximizing NEI at different water velocities. In Chapter Three I use the results of the velocity experiments from Chapter One to develop models that predict optimal foraging velocities for coho and steelhead based on NEI rates. I also include a discussion of factors other than foraging abilities that may influence habitat selection and segregation.

CHAPTER ONE

THE INFLUENCE OF WATER VELOCITY ON PREY DETECTION AND CAPTURE BY DRIFT-FEEDING COHO SALMON AND STEELHEAD[1]

[1]John J. Piccolo, Nicholas F. Hughes, and Mason D. Bryant

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Abstract. We examined the effects of water velocity on the geometry and dynamics of prey capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*). We used three-dimensional video analysis of feeding experiments to test the hypothesis that prey capture probability decreases as water velocity increases. We also tested for differences between coho and steelhead in capture probability, prey detection distance, prey interception speed, and return speed. We found prey capture probability decreased from ~ 65% to 10% with an increase of water velocity from 0.29 to 0.61 $m \cdot sec^{-1}$; this relationship was similar for both species. Coho and steelhead also showed similar decreases in prey detection distance and in capture probabilities within the capture area as velocity increased. The decrease in detection distance was largely in the upstream direction, resulting in a shorter, but not narrower, prey detection field. Prey were detected throughout the detection field, rather than at the maximum detection distance. These findings suggest that information processing may limit prey detection. Fish intercepted prey at their maximum sustainable swimming speed (Vmax) at all velocities. At slower velocities they returned to the focal point at the water current speed. At faster velocities return speeds were faster than Vmax, indicating potentially large increases in energetic cost because of anaerobic swimming. We conclude that faster water velocity reduces prey capture probability for coho and steelhead, but that species-specific differences in capture ability are not responsible for velocity-based habitat segregation.

Keywords: water velocity; prey capture; prey detection; drift-feeding; foraging; coho salmon; steelhead.

INTRODUCTION

Stream salmonids often forage by drift feeding, maintaining a position in the stream channel and capturing invertebrate prey as it is delivered by the current (Bachman 1984, Fausch 1984, Hughes and Dill 1990). For drift feeders, selecting a position in faster water is assumed to be a trade-off between the benefit of encountering more prey and the cost of foraging in faster water (Fausch 1984). Ecologists have incorporated drift feeding into energetics-based models that have been successful in predicting stream salmonid distribution (Fausch 1984, Hughes and Dill 1990, Hughes 1992, Guensch et al. 2001), energy intake (Hill and Grossman 1993, Hughes et al. 2003), and growth (Hill and Grossman 1993, Hughes 1998, Hayes et al. 2000, Nislow et al. 2000, Hughes et al. 2003). Water velocity plays an important role in these models because it determines both the prey encounter rate and the capture probability for a fish at a given stream position (Fausch 1984, Hill and Grossman 1993, Hughes et al. 2003). To date, researchers have found that drift-foraging models are more sensitive to changes in benefits (e.g. prey density or prey encounter rate) than they are to changes in costs (Hughes and Dill 1990, Hill and Grossman 1993, but see Hughes et al. 2003 for a discussion of prey capture costs). This underscores the importance of identifying how water velocity affects the fish's ability to detect and capture prey. Hughes et al. (2003) noted that developing models to more accurately predict energy intake rates of drift-feeders will require a better understanding of how habitat factors such as water velocity influence prey detection and capture.

Despite the importance of water velocity in drift-foraging models, few studies have addressed how velocity influences prey capture in drift-feeding salmonids. Increasing velocity may reduce prey capture distance and the size and width of the prey capture area (Godin and Rangeley 1989, Hill and Grossman 1993, O'Brien and Showalter 1993). O'Brien et al. (2001) found increasing water velocity decreased prey capture efficiency as well as capture distance for Artic grayling (*Thymallus arcticus*), but they did not find an expected increase in foraging rate. They suggested this may be due to a tradeoff between increasing encounter rate and decreased prey detection ability as water velocity increases. They also found that search and interception times were not affected by water velocity. This is important because drift-foraging models rely on estimates of search and handling time (Hayes et al. 2000, Guensch et al. 2001, Hughes et al. 2003), but to date little is known about how water velocity influences the dynamics of prey capture.

Although drift-foraging models have been used to predict habitat selection for two or more sympatric species (Fausch 1984, Hill and Grossman 1993, Braaten et al. 1997, Guensch et al. 2001), there have been no comparisons of the effects of water velocity on two sympatric drift feeders. This represents a gap in our understanding of stream salmonid habitat selection because velocity-based habitat segregation has been documented for a number of sympatric pairs of salmonids (Hartman 1965, Everest and Chapman 1972, Gibson et al. 1993, Bremset and Berg 1999). If fish segregate habitat based on their potential to maximize net energy intake at their respective positions (e.g. Fausch 1984, Hill and Grossman 1993) it ought to be possible to identify the mechanism that allows them to do so at different velocities. Werner and Hall (1979), for example,

showed that differences in body morphology among three species of sunfish facilitated habitat segregation based on foraging efficiency. Although differences in body morphology have been suggested as one explanation for habitat segregation in stream salmonids (Bisson et al. 1988), no experimental tests have confirmed this.

Juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*) occur sympatrically in freshwater streams (Groot and Margolis 1991, Behnke 1992, Nakano and Kaeriyama 1995), where they often drift feed (Everest and Chapman 1972, Nielsen 1992). Although they are found within the same stream reaches they have been documented to segregate microhabitat, with coho using pools and steelhead riffles (Hartman 1965, Bisson et al. 1988, Bugert and Bjornn 1991). Bisson et al. (1988) proposed that coho may be better adapted to forage in pools because they have a laterally-compressed body form with long median fins, which facilitates rapid turning and acceleration. Steelhead may be better adapted to foraging in riffles because they have a more cylindrical body form with shorter median fins, which minimizes drag during foraging maneuvers.

Our objective was to assess the influence of water velocity on prey detection and capture by juvenile coho and steelhead. We used three-dimensional video analysis of stream-tank foraging experiments to test these hypotheses: 1) prey capture probability declines with increasing water velocity, and 2) there are species-specific differences in capture probability, prey detection distance, prey interception speed, and speed of return to the focal point, that might facilitate foraging in their respective preferred habitats.

METHODS

Stream tank

We constructed a variable-depth and -velocity stream tank to allow precise adjustment of water velocity (Fig. 1.1). The experimental arena measured 1.5 m long x 1 m-wide x 0.3 m-deep, enclosed at each end with mesh screens. A Plexiglas window on one side allowed us to videotape the experiments. The remainder of the arena was painted a light blue-green color. A 0.10 x 0.10-m grid of dots were drawn on the viewing window and the back wall to allow 3-D analysis of video data (see below). The substrate was ~ 0.01-m diameter gravel. One flat, ~ 0.1-m diameter rock was placed near the center of the tank to serve as a focal point. Prey were delivered through the upstream screen via any one of 20 plastic feeder tubes (6.25-mm diameter) arranged in two layers of 10 each, equally-spaced, at layers 0.1- and 0.2-m deep. Uneaten prey were filtered out by a 0.625-mm mesh stainless steel screen so they could not recirculate.

Experimental protocol

Nineteen wild fish of each species were collected from the West Fork of the Situk River near Yakutat, Alaska in June 2001. Fish measured 70-80 mm fork length, which are presumed to be age I+ based on length-frequency data (Lohr and Bryant 1999, Halupka et al. 2000). All fish were collected from the same stream reach. Fish were shipped via air to Juneau, Alaska, and held in flow-through circular tanks. They were fed maintenance rations of frozen brine shrimp.

We conducted our experiments in a covered outdoor lab facility at the NOAA National Marine Fisheries Service Auke Bay Laboratory, Juneau Alaska, September-October 2001. Freshwater was supplied by a subsurface line from Auke Lake (mean water temperature was 10.46 °C (SD = 0.84); mean dissolved oxygen was 7.78 $mg \cdot l^{-1}$ (SD = 0.66); mean pH was 7.9 (SD = 0.21); mean turbidity was 0.36 NTU (SD = 0.16). Photoperiod was maintained at 18 h day and 6 h night.

We selected five water velocity treatments ranging from the minimum at which fish would hold station and drift feed to near the maximum published value for 75-mm juvenile coho and steelhead (Everest and Chapman 1972, Beecher et al. 1993). Treatments were 0.29, 0.39, 0.48, 0.54, and 0.61 $m \cdot sec^{-1}$ mean water column velocity (measured at a point 0.20 m upstream from the focal point). At each treatment level we made a detailed map of water velocity in the experimental arena by measuring velocity in 0.10 x 0.10-cm grids at three cross-sections, used for calculations of prey and fish speed (see *Data analysis* below).

We randomly selected 5 fish of each species, ranging from 75-80-mm fork length, and paired by size between species. Experimental fish were held individually in 1 x 0.3 x 0.3-m flow-through raceways during the experimental period. Each fish was tested individually at each velocity, assigned in a random order with two days rest between treatments. Two species pairs of fish were tested each day, and the entire series of feeding trials was completed in as few days as possible to minimize any effects of time or growth (fish grew an average of 3.4 mm during experimental period). Fish were not fed for 24 hours prior to a feeding trial to ensure they would be motivated to feed.

Each fish received a 15-minute "warm-up" feeding trial to acclimate them to the experimental arena. Fish acclimated well to the experimental protocol, usually selecting a position behind the focal point rock and feeding within a minute of being introduced to the tank. For each feeding trial a fish was netted from its individual raceway and quickly released into the experimental arena at the slowest velocity. Velocity was stepped up gradually to the treatment level. A fish was observed to feed on at least one prey before the velocity was increased to the next level. When the test velocity was reached and the fish was observed to be actively feeding, the trial began. A feeding trial consisted of 100 individual prey being fed to a fish over a 25 minute period (4 prey · min^{-1}). Prey were adult brine shrimp cut to 2-mm length to ensure that the fish's reaction distance to the prey would be less than half of the tank width (Dunbrack and Dill 1984). Prey were randomly assigned to one of the 20 feeder locations, and were fed at random times within each 15-sec interval. At the conclusion of the experiment fish were fed extra prey to be sure that they had not become satiated, and they were always observed to eat more prey.

We recorded our feeding trials on miniDV cassettes using two Sony GVD900 tape recorders and two Sony EVI 334 video cameras. Cameras were positioned at ~ 90 degrees from each other relative to the fish focal point to facilitate 3-D analysis.

Data analysis

All prey capture maneuvers for each fish were digitized using custom-designed computer software (Hughes and Kelly 1996). This allowed us to count the number of prey captured, and to get the videotape timecode and 3-D coordinates (x = upstream-

downstream, y = across-stream, and z = vertical) for the nose and tail of the fish at the start, capture, and return point of each maneuver. To obtain the *x,y,z,* coordinates and times for each prey capture maneuver we:

1) Identified a prey capture maneuver on the tape, and obtained the *x,y,z,* coordinates and time for the focal point location.
2) Forwarded the tape to obtain the *x,y,z,* coordinates and time of the capture location when the fish closed its mouth on the prey.
3) Defined the difference of these times as the prey interception time.
4) Estimated interception distance by assuming that the fish initiated a maneuver as soon as it detected a prey, and that it swam in straight line to capture it. Once the fish leaves its focal point and enters the water column it is displaced downstream at the same rate as is the prey; therefore interception distance = detection distance.
5) Estimated the *x,y,z,* coordinates of the detection location by back-calculating the distance the prey had traveled along the x-axis from the capture location during the interception time, and assuming the y and z position did not change.
6) Calculated the detection distance as the distance between the focal point coordinates (i.e. x_1, y_1, z_1) and the detection coordinates (i.e. x_2, y_2, z_2) using Pythagoras' theorem as follows:

$$\text{Distance} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

7) Defined return time as the time taken from interception until the fish returned to the focal point.

8) Estimated the return distance by adding the amount of downstream (x-axis) displacement the fish experienced during the return time to the focal point location, and calculating the distance between the capture location coordinates and this upstream point using Pythagoras' theorem.

9) We calculated interception and return speeds by dividing distances by times.

Front-, side-, and top-view figures of prey detection and capture locations were created by plotting the appropriate coordinates (front, y,z; side, x,z; top, x,y) after normalizing all focal point locations to the median and pooling by species ($N = 5$).

We used linear regression (Zar 1999) to assess the effect of water velocity on prey capture probabilities and feeding performance measures. The following regressions were fitted separately for coho and steelhead: 1) prey capture probability vs. water velocity, 2) mean prey detection distance vs. water velocity, 3) mean prey interception speed vs. water velocity, and 4) mean return speed vs. water velocity. We tested for significance of the individual regressions ($\alpha = 0.05$), and compared the slopes and elevations between the species using Student's t-tests ($\alpha = 0.05$, two-tailed) to test the null hypotheses that 1) the slopes and 2) and elevations between two regression lines are equal (Zar 1999).

RESULTS

Prey capture probability

We found significant negative relationships between prey capture probability and water velocity for both coho ($P = <0.001$, $r^2 = 0.90$) and steelhead ($P = <0.001$, $r^2 = 0.85$) (Table 1.1. Fig. 1.2). Neither the slopes ($P = 0.34$) nor the elevations ($P = 0.68$) of the regression lines differed significantly between coho and steelhead (Table 1.1. Fig. 1.2). Overall prey capture probability for both species was reduced from 65 to 25% with a water velocity increase from 29 to 55 $cm \cdot sec^{-1}$, with both species averaging nearly identical probabilities at these velocities. At the fastest velocity (0.61 $m \cdot sec^{-1}$), however, the mean capture probability for coho was half that of steelhead (7 vs. 14%).

3-D analysis: Prey detection

We also found significant negative relationships between prey detection distance and water velocity for both coho ($P = <0.001$, $r^2 = 0.44$) and steelhead ($P = <0.001$, $r^2 = 0.69$) (Table 1. Fig. 1.3A). Neither the slopes ($P = 0.47$) nor the elevations ($P = 0.13$) of the regression lines differed significantly between coho and steelhead (Table 1.1. Fig. 1.3A). Prey were detected throughout the reaction volume rather than on the surface (i.e. at the maximum detection distance), and mean detection bearing increased with increasing velocity (Figs. 1.4, Fig. 1.5). The reduction in detection distance was largely due to a reduction in the mean upstream (x-axis) distance, rather than in the lateral (y-axis) or vertical (z-axis) distances (Fig. 1.5).

Prey capture

We did not find significant relationships between prey interception speed and water velocity for either coho ($P = 0.46$, $r^2 = 0.02$) or steelhead ($P = 0.15$, $r^2 = 0.09$) (Table 1.1. Fig. 1.3B). Neither the slopes ($P = 0.72$) nor the elevations ($P = 0.11$) of the regression lines differed significantly between coho and steelhead (Table 1.1. Fig. 1.3B). At all velocities coho and steelhead intercepted prey at close to their predicted maximum sustainable swimming speeds (Vmax, 0.41 m · sec^{-1}), as calculated using equations for juvenile sockeye salmon of the same size (Brett and Glass 1973) (Fig. 1.3B). The mean *x*-coordinates for prey capture location were located farther downstream with increasing velocity (Fig. 1.5) At the slowest velocity fish of both species intercepted about an equal percentage of prey both upstream and downstream of the focal point, and at faster velocities nearly all prey were intercepted downstream of the focal point (Fig. 1.5). Capture probabilities declined uniformly within the capture area (Fig. 1.6).

Return to the focal point

We found significant positive relationships between speed of return to the focal point and water velocity for both coho ($P = <0.001$, $r^2 = 0.93$) and steelhead ($P = <0.001$, $r^2 = 0.95$) (Table 1.1. Fig. 1.3C). Neither the slopes ($P = 0.83$) nor the elevations ($P = 0.38$) of the regression lines differed significantly between coho and steelhead (Table 1.1. Fig. 1.3C). Fish retuned to the focal point at approximately the same speed as the current until it exceeded their Vmax, after which they exceeded current speed. At the faster velocities

fish tended to swim quickly to the substrate after a prey capture, and then swim along the bottom back to the focal point.

DISCUSSION

The negative effect of increasing water velocity on prey capture probability by coho and steelhead appears to be due to two factors: 1) a decrease in prey detection distance, and 2) a decrease in capture probabilities within the capture area. The first of these has been reported for drift feeding salmonids (Hill and Grossman 1993, O'Brien and Showalter 1993) and also for drift-feeding coral reef fish (Kiflawi and Genin 1997). In our experiments detection distance decreased more in the upstream, rather than the across-stream, direction, whereas O'Brien and Showalter (1993) and Kiflawi and Genin (1997) reported a narrowing of the detection area. The prey detection area has been described as a pie-shaped wedge projecting forward from the fish's focal point, delimited upstream by their reaction distance and across-stream by the search angle (Hughes and Dill 1990, O'Brien and Showalter 1993, Kiflawi and Genin 1997). Our results show that the detection area may be reduced in an upstream rather than across-stream direction, resulting in a shorter, not narrower, piece of pie.

Decreased prey detection distance and probability with increasing velocity suggests that search efficiency is an important factor in limiting prey capture success. Hughes et al. (2003) proposed that velocity-dependent prey detection limitations might be one explanation for their model's over-prediction of foraging rate in adult brown trout. Similarly, Kiflawi and Genin (1997) proposed that a velocity-dependent decline in prey detectability and/or capture success within the foraging area might be responsible for their model's overprediction of foraging rates of drift-feeding coral reef fish at faster

velocities. Our results - a lack of velocity-dependent narrowing of the detection area, prey detections throughout rather than on the surface of the detection area, and a uniform reduction in capture probabilities – support this idea of velocity-dependent prey detection limitations. Because our fish searched an area of similar height and width at all velocites (i.e. the maximum detection distance declined little), the volume of water searched increased nearly proportional to water velocity. Searching a larger volume of water for faster-moving prey would almost certainly decrease the probability of detection if information processing ability was limiting. Hughes et al. (2003) note that no exisiting model of prey detection can explain spatial variability in prey detection; our results show that search volume and prey speed need to be incoroporated into such models. Our experimental design, with known prey introduction locations and rates and variable water velocities, offers an effective means of testing prey detection models.

Velocity-dependent reductions in the size of the capture area, and in capture probablitites within this area, have important implications for models that predict foraging, growth, and habitat selection in stream salmonids. Hughes et al. (2003) found that their model of drift foraging in brown trout overestimated foraging and gross energy intake rates by a factor of two. They showed that most of the model's inaccuracy was due to an incorrect assumption that prey capture probablities are high and uniform across the fish's capture area. In our experiments the highest mean prey capture probablilities were relatively low (0.65), and they decreased with increasing water velocity. In addition, we found a velocity-dependent reduction in the mean, but not in the maximum, capture distance. This suggests that capture probabiliites and capture distances of fish

foraging in areas of mixed velocities vary considerably across the foraging area. Until adequate models of prey detection are developed, drift foraging models might be improved by incorporating velocity-dependent capture probabilites, and median, rather than maximum, capture distances.

A velocity-dependent narrowing of the prey detection area has been an essential part of drift foraging models, used to predict the effects of water velocity on energy intake and consequently, for predicting an optimum feeding velocity (Hughes and Dill 1990, Kiflawi and Genin 1997). In order to explain this narrowing, these models have assumed that: 1) prey are detected at the fish's reaction distance, 2) prey are captured upstream of the fish's focal point, and 3) capture probability is 100% for all energetically favorable prey. Our results, and those of O'Brien and Showalter (1993) and Hughes et al. (2003) have shown this first assumption to be false. Although our maximum detection distance corresponds closely to the reaction distance for coho of this size reported by (Dunbrack and Dill 1984), the mean was less than this distance and it decreased with increasing water velocity. Our results also corraborate reseach that shows the second assumption to be false (Hughes et al. 2003), and further, they demonstrate that the downstream distance and the proportion of prey captured downstream of the focal point is velocity dependent. Lastly, our results show the third assumption to be false, because prey capture probability within the foraging area never exceded 70% This, coupled with the fact that we did not find a velocity-dependent narrowing of the foraging area as previously reported (O'Brien and Showlater 1993, Kiflawi and Genin 1997) may lend insight into why foraging models have successfully predicted habitat selection despite incorporating these false

assumptions: It is possible that the additional prey detected and captured both more laterally and further downstream than the models allow represent an approximately equal tradeoff for those prey within the foraging area that the models wrongly assume are captured.

Fish of both species intercepted prey at close to their predicted Vmax at all velocities. One explanation for this is that at Vmax fish should minimize their handling time while not aquiring oxygen debt as they would by swimming at burst speed (Puckett and Dill 1984). These results agree with Hughes et al.'s (2003) model assumption that fish should intercept prey at Vmax. They differ from their results for adult brown trout, however, which tend to intercept prey at the same speed at which the prey drift (i.e. the same as water velocity). Because our fish did not increase interception speed at faster velocities, downstream displacement for prey captures increased as water velocities increased. Although this is mitigated somewhat by decreased prey detection distance at faster velocities, the net effect is a greater return distance as velocity increases.

Unlike interception speeds, return speeds were velocity dependent, with fish swimming at increasingly faster speeds at faster water velocities (again with no difference between species). At velocities less than Vmax, fish returned to the focal point at the same speed as water velocity. At velocities faster than Vmax they swam faster than water velocity, thereby incurring significant oxygen debt by burst swimming (Pucket and Dill 1984) . There were velocity-dependent behavioural differences as well, with fish at slow velocities apparently searching for prey while returning to the focal point and fish at fast velocities burst swimming towards the substrate and returning the

remainder of the distance to the focal point along the velocity shelter of the substrate. Models of drift feeding have often disregarded the costs of prey capture as relatively insignifcant (e.g. Hughes and Dill 1990; Hill and Grossman 1993). Our results suggest that return costs may be considerable if fish are foraging in areas of velocity greater than their Vmax.

In optimal foraging models fish should not pursue prey that are not profitiable (Charnov 1976). Because we estimated prey detection locations from capture locations, our analyis of prey detection is for only those prey that were captured. At the faster velocities, however, we noted instances in which fish appeared to begin a manuever when a prey was passing, but then decided to return to the focal point. This suggests that some prey may have been dropped from the diet based on profitability, because fish were required to burst swim to return to the focal point at fast velocites. One method that might prove useful for further investigating this is to get a close-up image of the fish with a third camera. Prey of various profitability could then be fed, and detection noted by observing if the fish trained its eye on the passing prey.

Our results for juvenile salmonids show increases in detection angles and interception speeds with increasing velocity. This differs from results reported for adult salmonids (O'Brien and Showalter 1993, Hughes et al. 2003). One explanation is that juvenile fish might continue to search relatively larger areas (i.e. greater angles), and have faster interception speeds in order to catch as many prey as possible to maximize growth rates. Adult fish might be on lower growth trajectories, or they might be more likely to weigh other concerns (e.g. predation risk) in formulating their foraging strategies. Also, relative

to body length, water velocities and interception distances are much greater for the juvenile fish in our study versus adult grayling (O'Brien and Showalter 1993) or brown trout (Hughes et al 2003). Our fish foraged at water velocities of 3-8 body lengths·sec^{-1} and intercepted prey at a median distance of 3-4 body lengths. The adult fish foraged at velocities of 1-2 body lengths·sec^{-1}, and they intercepted prey at a distance of 1-2 body lengths. It is likely, therefore, that water velocity influences both the costs and benefits of foraging in juvenile fish differently than it does in adults. This is an area of particular interest for biologists interested in predicting habitat use, because stream salmonids have been shown to move into faster and deeper water as they grow (Everest and Chapman 1972, Heggenes et al. 2002).

We think it is unlikely that differential prey capture ability can explain velocity-based habitat segregation between coho and steelhead. The relationship between prey capture probability and water velocity was very similar for both species, and manuever characteristics such as detection distance, and interception and return speeds were nearly identical, which suggest that both species use very similar search and capture methods while drift feeding. Although differences in prey capture ability may not facilitate habitat segregation between coho and steelhead, it is possible differences in the prey capture costs are responsible. In Chapther Three we test this hypothesis using models of net energy intake rate. Another explanation is that life history differences between the species (e.g. different foraging strategies or growth trajectories) influence the temporal and spatial aspects of foraging. This is also discussed in Chapter Three. A third explanation is that another aspect of pool vs. riffle habitat (e.g. depth or cover) might

facilitate habitat segregation by coho and steelhead. In Chapter Two we present experiments that assess the effects of water depth on prey detection and capture by coho and steelhead.

CONCLUSIONS

We found a strong negative relationship between prey capture probability and water velocity for coho and steelhead, but little difference between the species. We also found that maneuver characteristics for both species were similar. We conclude that water velocity has a substantial effect on prey capture probabilities, but that factors other than prey capture abilities must be responsible for habitat segregation between coho and steelhead. The reduction in prey capture probability appeared to be due to velocity-dependent reductions in: 1) the size of the prey detection area, and 2) capture probabilities within the capture area. Most of the reduction in size was due to a reduction in the mean upstream detection distance. This differs from other published accounts in which prey detection fields narrowed with increasing water velocity. The reduction of capture probabilities within the capture area suggests that information processing may be limiting prey detection. This provides support for the hypothesis that limitations in prey detection, rather than maneuver constraints, may determine the size of the prey capture field. Fish intercepted prey at close to Vmax at all velocities. At fast velocities fish returned to the focal point considerably faster than Vmax, indicating an increase in energetic cost resulting from anaerobic swimming.

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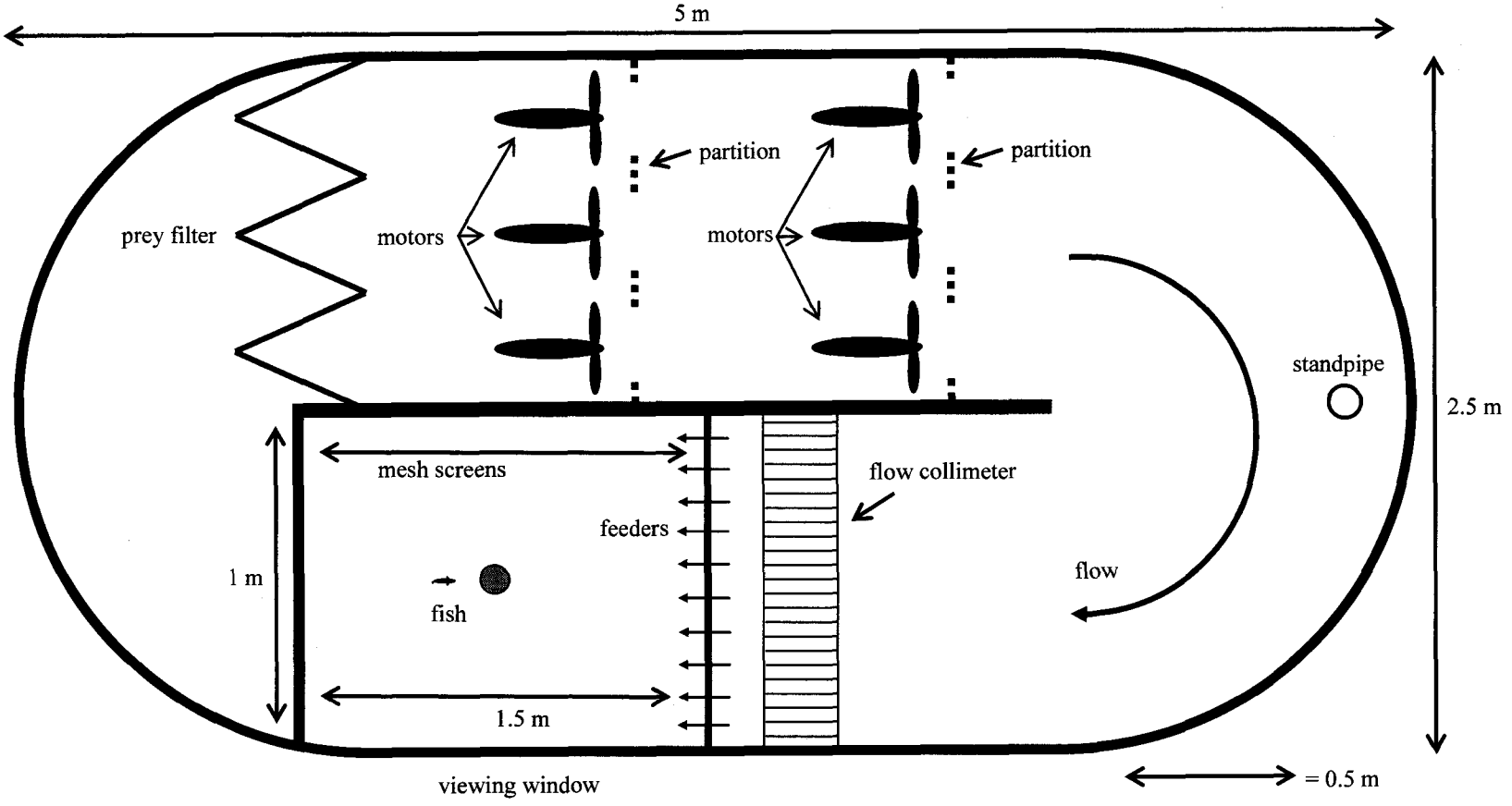

Figure 1.1. Top-view diagram of the stream tank, drawn to approximate scale. Water velocity was provided by six Minn Kota EM44 electric trolling motors powered by 120-V AC to 12-V DC transformers. The motors raised the water pressure head on the downstream side of the partitions, pushing water through the flow collimator (0.04-m diameter PVC pipe), providing relatively uniform velocity across the tank. Filtered water was added continuously to maintain water quality and it drained through the standpipe maintaining a depth of 0.30 m. Overhead light was provided by a 150-watt full spectrum bulb, shaded to reduce glare. Light intensity was 500 lux at the water surface above the focal point.

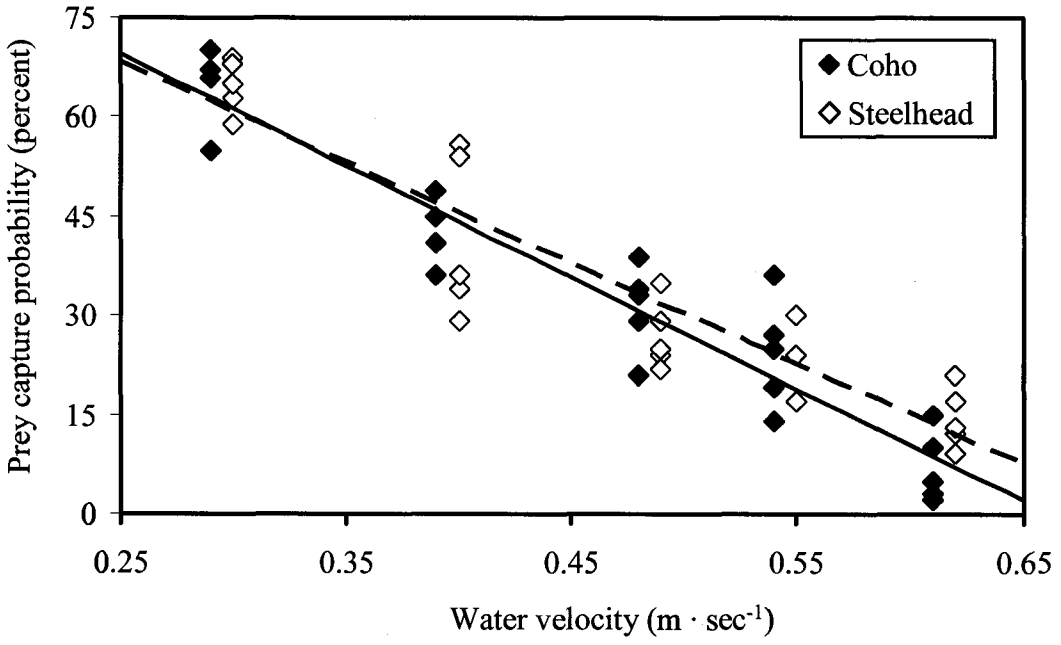

Figure 1.2. Prey capture probability vs. water velocity for coho (solid diamonds, line) and steelhead (open diamonds, dashed line). Regression equations and significance tests are found in Table 1.1. Each data point represents the capture probability for one fish for a 25-minute feeding trial (n = 5 of each species). Each fish was tested at each velocity, assigned in a random order. Steelhead data points are offset by +0.01 m · sec^{-1} for visual clarity.

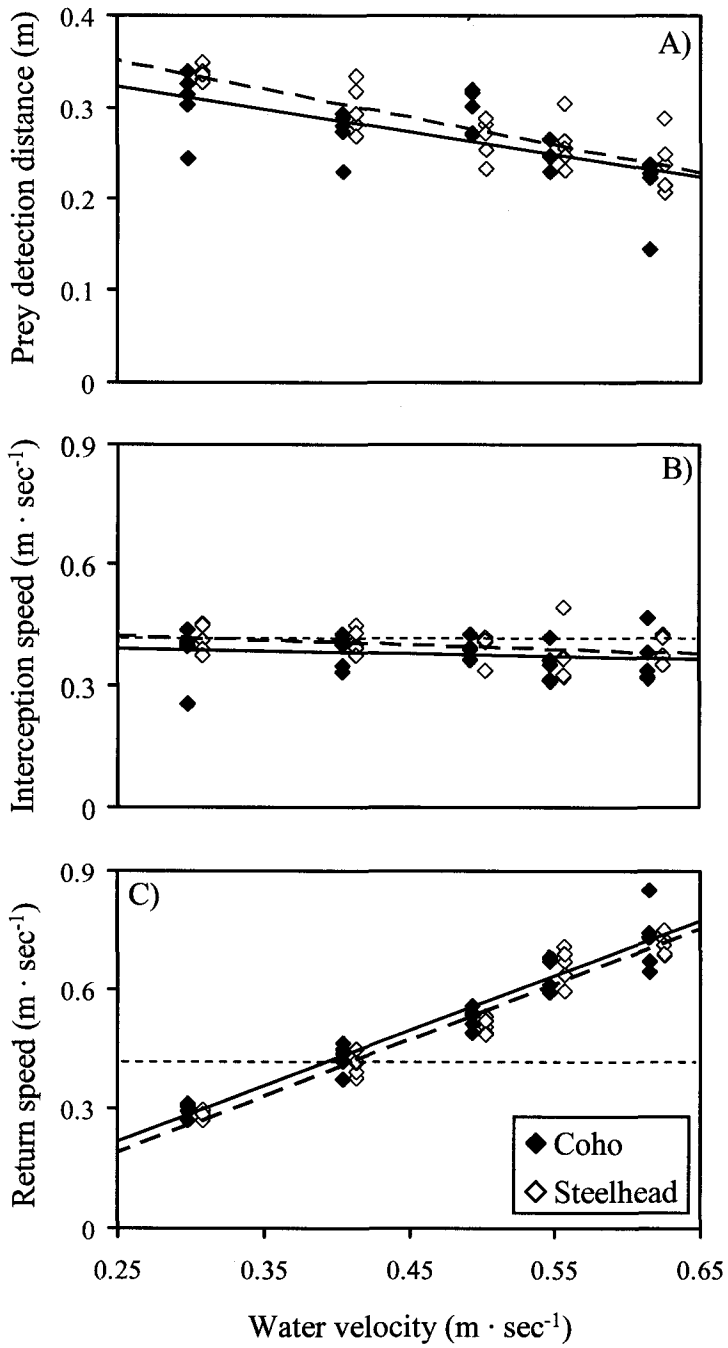

Figure 1.3. Mean: A) prey detection distance, B) interception speed, and C) return speed, vs. water velocity for coho (solid diamonds, lines) and steelhead (open diamonds, dashed lines). Equations and significance tests for regressions are found in Table 1.1. Each data point represents the mean value of the *y* variable for one fish for a 25-minute feeding trial (n = 5 of each species). The finely-dashed horizontal lines in panels B) and C) are the predicted maximum sustainable swimming speeds for coho and steelhead. Steelhead data points are offset by +0.01 m · sec^{-1} for visual clarity.

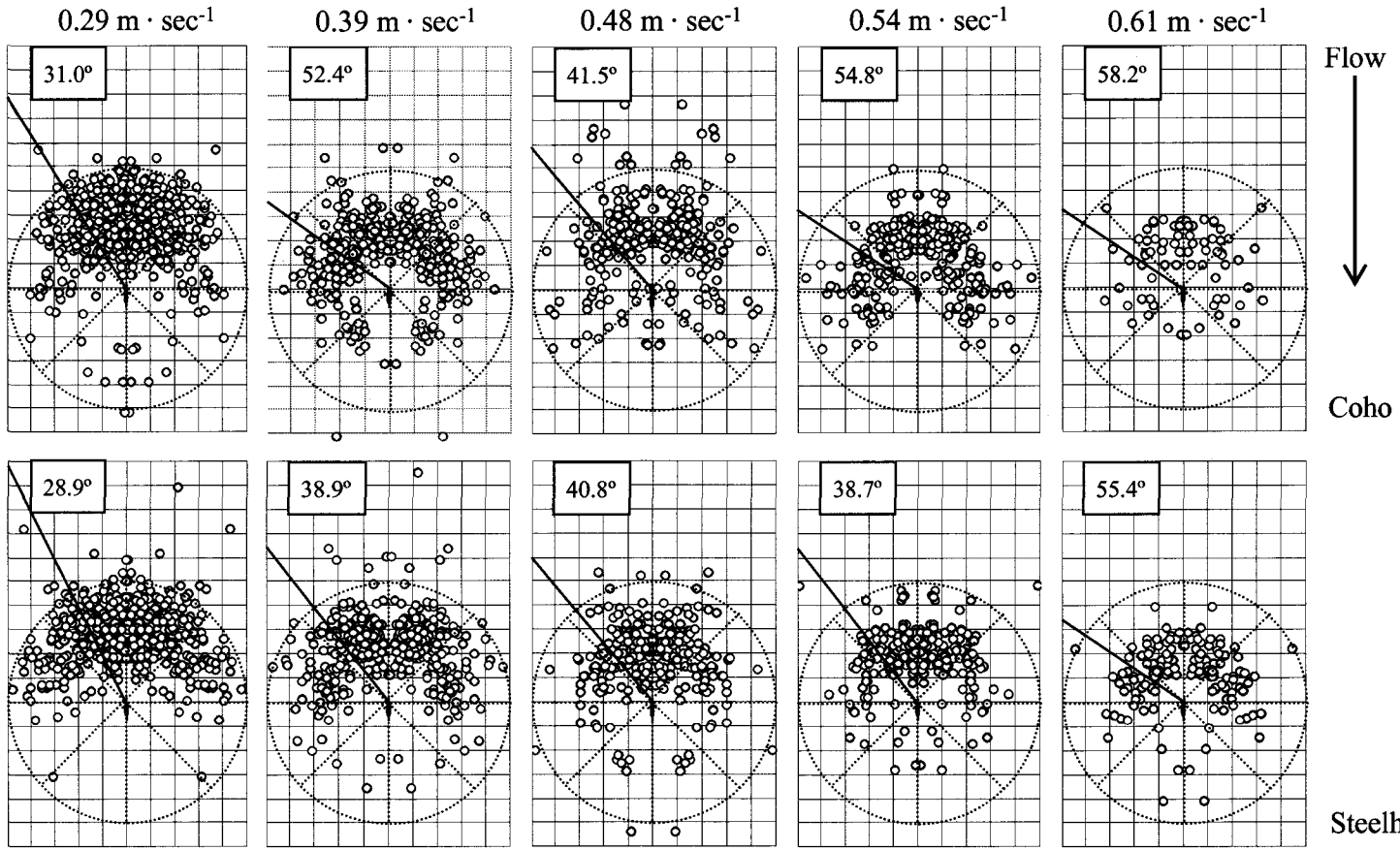

Figure 1.4. Top view of prey detection locations (*x,y* coordinates) for coho (top) and steelhead (bottom) at five water velocities, listed at the top of the figure. Data are pooled for all fish (n = 5 of each species) tested at each velocity. Each circle represents one prey capture. Water flow from top to bottom of figure. Dark lines to the left of the fish are mean prey detection angles (bearings in box) with 0° upstream and 180° downstream of fish. Detection locations have been rotated into the horizontal plane retaining distance and bearing.

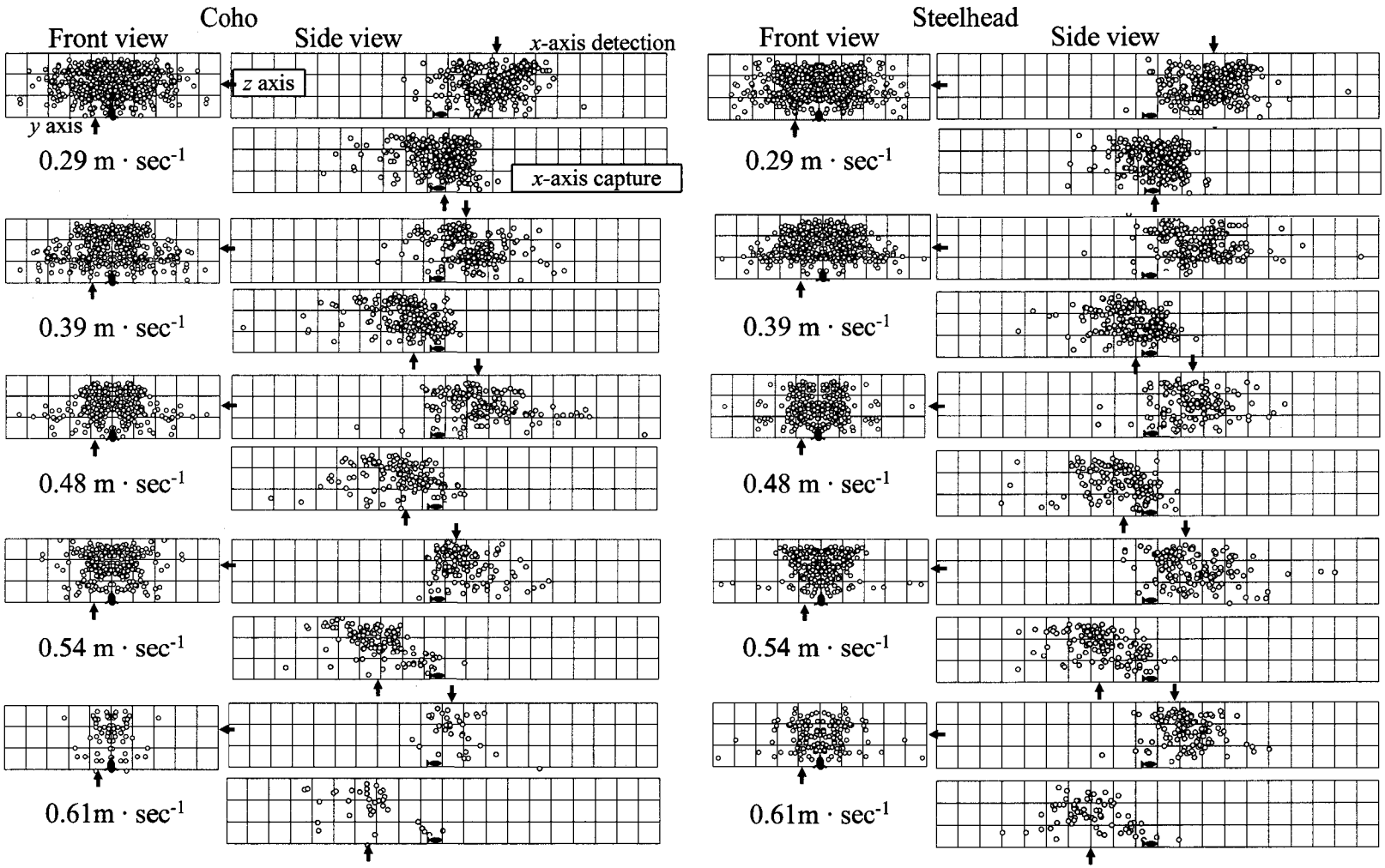

Figure 1.5. Front and side views of prey detection and prey capture locations for coho (left) and steelhead (right). Grid squares are 0.10 x 0.10 m. Front view is the same for detection and capture locations; top side view in each panel is detection and bottom is capture. Arrows indicate mean *x*, *y*, *x*, axes detection and capture distances. Data are pooled for 5 of each species tested at each velocity. Each circle represents one prey capture.

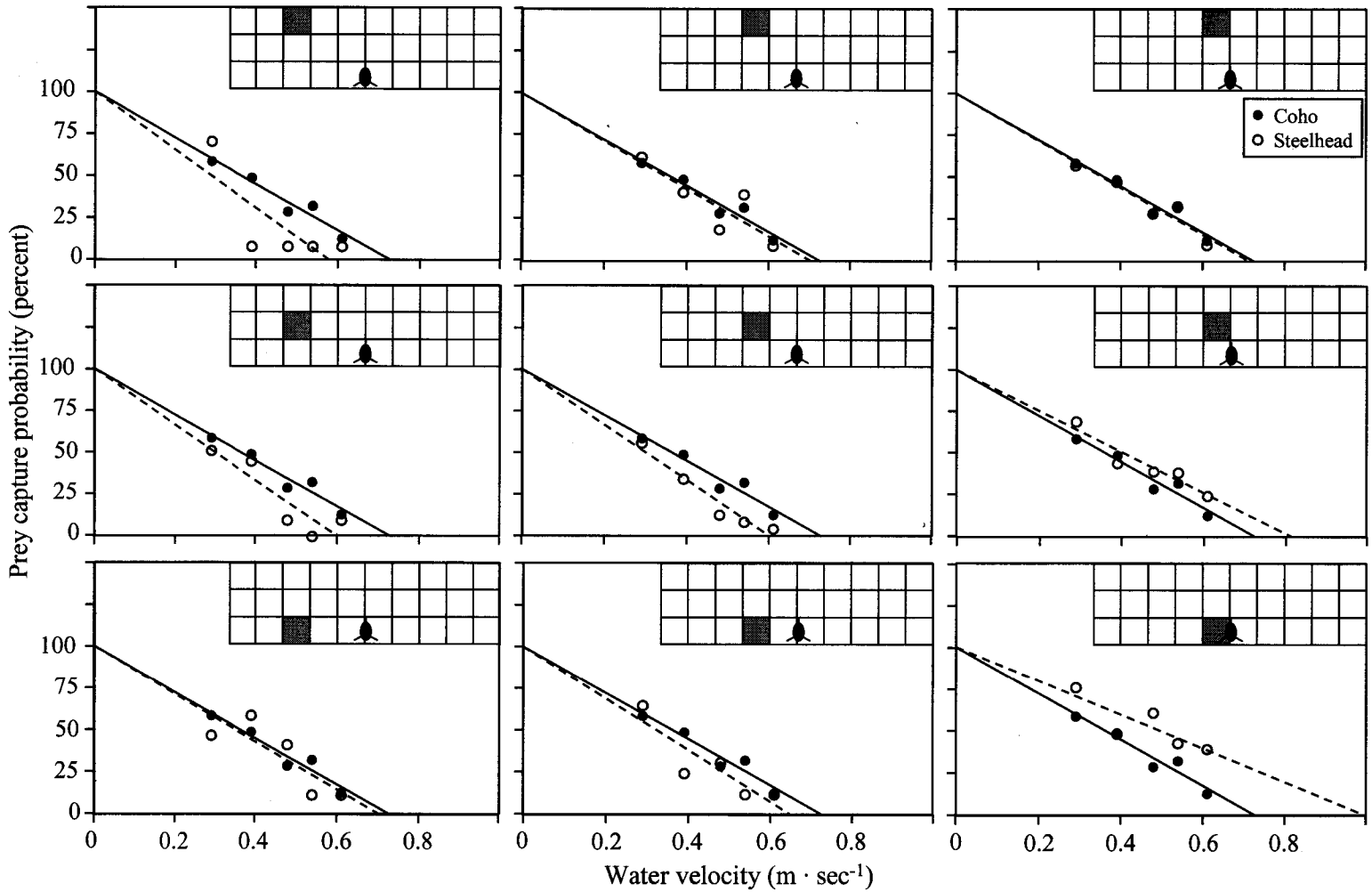

Figure 1.6. Capture probability vs. water velocity for coho (solid circles, lines) and steelhead (open circles, dashed lines) for each 0.10 x 0.10 m square of the capture area shown by gray shading in the front view figure. Each data point represents the mean capture probability of five fish.

Table 1.1. Regression equations and significance tests for prey capture characteristics of juvenile coho salmon and steelhead ($N = 5$). Regression x variable in all equations is water velocity ($m \cdot sec^{-1}$). F values are for significance of individual species' regressions (* indicates $P < 0.001$). Non-significant P values (>0.05) for t-tests indicate failure to reject the null hypothesis that slopes or elevations of species' regression lines are equal (Zar 1999).

				test for equal slopes		test for equal elevations	
Regression y variable	Regression equation	r^2	F value	t value	P value	t value	P value
Number of prey captures							
Coho	$y = -169.2x + 112.0$	0.90	198.08*	0.96	0.34	0.42	0.68
Steelhead	$y = -151.9x + 104.8$	0.85	128.03*				
Prey detection distance (cm)							
Coho	$y = -0.25x + 0.38$	0.44	17.86*	0.72	0.47	1.56	0.13
Steelhead	$y = -0.30x + 0.42$	0.69	50.18*				
Interception speed (cm sec)							
Coho	$y = -0.07x + 0.41$	0.02	0.57	0.36	0.72	1.65	0.11
Steelhead	$y = -0.11x + 0.45$	0.09	2.23				
Return speed (m sec)							
Coho	$y = 1.37x - 0.11$	0.93	300.04*	0.22	0.83	0.89	0.38
Steelhead	$y = 1.39x - 0.13$	0.95	477.27*				

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Appendix 1.1. Results of experiments on the effect of water velocity on juvenile coho and steelhead. Number of prey captures are the results of each fish at each velocity (n = 5 for each species). Mean values are for multiple observations of detection distance, and interception and return speed for each fish.

Water velocity ($m \cdot sec^{-1}$)	Number of prey captures		Mean Prey detection distance (m)		Prey interception speed ($m \cdot sec^{-1}$)		Speed of return to focal point ($m \cdot sec^{-1}$)	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
0.29	66	63	0.31	0.33	0.40	0.41	0.30	0.27
0.29	67	69	0.33	0.33	0.44	0.45	0.27	0.27
0.29	70	59	0.34	0.35	0.41	0.39	0.29	0.29
0.29	55	65	0.24	0.34	0.26	0.37	0.31	0.30
0.29	67	68	0.30	0.34	0.40	0.45	0.29	0.29
0.39	41	29	0.28	0.28	0.41	0.40	0.46	0.38
0.39	49	56	0.29	0.33	0.42	0.45	0.37	0.39
0.39	45	54	0.29	0.32	0.40	0.39	0.44	0.41
0.39	36	34	0.27	0.27	0.33	0.37	0.42	0.42
0.39	36	36	0.23	0.29	0.35	0.43	0.45	0.45
0.48	34	24	0.30	0.23	0.39	0.33	0.54	0.53
0.48	39	35	0.32	0.28	0.43	0.42	0.49	0.50
0.48	29	22	0.27	0.29	0.36	0.41	0.51	0.49
0.48	33	29	0.32	0.27	0.39	0.41	0.56	0.52
0.48	21	25	0.27	0.25	0.42	0.41	0.54	0.49
0.54	19	24	0.23	0.23	0.35	0.32	0.67	0.67
0.54	25	24	0.27	0.26	0.31	0.32	0.61	0.64
0.54	27	30	0.25	0.31	0.42	0.49	0.59	0.60
0.54	14	17	0.25	0.26	0.31	0.37	0.68	0.71
0.54	36	30	0.27	0.25	0.36	0.37	0.68	0.69
0.61	3	9	0.23	0.29	0.32	0.37	0.85	0.73
0.61	15	21	0.24	0.24	0.38	0.37	0.73	0.71
0.61	10	12	0.22	0.21	0.34	0.42	0.74	0.69
0.61	2	17	0.14	0.22	0.32	0.35	0.65	0.69
0.61	5	13	0.24	0.25	0.47	0.42	0.67	0.75

CHAPTER TWO

THE INFLUENCE OF WATER DEPTH ON PREY DETECTION AND CAPTURE BY DRIFT-FEEDING COHO SALMON AND STEELHEAD[1]

[1]John J. Piccolo, Nicholas F. Hughes, and Mason D. Bryant

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Abstract. We used three-dimensional video analysis of feeding experiments to determine the effects of water depth on prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*). Depth treatments were 0.15, 0.30, 0.45, and 0.60 m. Prey capture probability for coho increased by only 6.2%, and it decreased < 1% for steelhead with increasing water depth,. The slopes of regression lines for capture probability vs. water depth for coho and steelhead did not differ significantly. In the deeper treatments, capture probabilities were lower in the surface layers than they were nearer the substrate, particularly at the lateral edges. Prey capture maneuver characteristics were very similar between the species, including significant positive relationships between water depth and both prey detection distance and interception speed. Speed of return to the focal point was not related to water depth. In the deeper treatments coho had greater capture probabilities nearer the surface than did steelhead, but it is unclear if this was a species difference, or one based on the relative amount of foraging experience fish had in the wild prior to capture. We used capture probabilities to predict prey capture rates for coho and steelhead, which increased linearly with water depth. We conclude that any benefit of foraging in deeper water is more likely due to increased prey encounter rate rather than to increased capture probability.

Keywords: water depth; prey capture; prey detection; foraging; habitat; segregation; drift-feeding; coho; steelhead.

INTRODUCTION

Juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*) have been shown to segregate stream habitat at both the stream reach (Hartman 1965, Bugert et al. 1991) and microhabitat (Fraser 1969, Johnston 1970, Allee 1981) scales. Within a stream reach, coho are often found in slower-velocity, deeper pools, whereas steelhead are often found in shallower riffles or runs (Hartman 1965, Bugert et al. 1991). Within microhabitats, coho have been shown to forage nearer the surface, and steelhead nearer the substrate (Fraser 1969, Johnston 1970, Allee 1981) Both species have also been shown to segregate along the water depth axis with other species of salmonids (Bravender and Shirvell 1990, Dolloff and Reeves 1990) or intraspecifically by size (Nielsen 1992, Harvey and Nakamoto 1997). Water depth is an important niche axis for segregation in other species of stream fish as well, both salmonid (Gibson and Power 1975, Bagliniere and Arribe-Moutounet 1985, Heggenes et al. 1999), and non-salmonid (Greenberg 1991, Reyjol et al. 2001, Jowett 2002, Hesthagen et al. 2004). Although depth is a commonly-measured feature of stream habitat (Bovee 1978), there has been little research on the underlying reason why fish select certain depths or why depth-based segregation is common in stream fish.

In Chapter Three we developed models of net energy intake (NEI) showing that velocity-dependent differences in foraging ability between coho and steelhead (e.g. Bisson et al. 1988) are not likely to explain habitat segregation. If water velocity is not the characteristic of pools and riffles that is responsible for habitat selection by coho and

steelhead, then what is? One possibility is water depth. Rosenfeld and Boss (2001) and Young (2004) have suggested that pools may be energetically more favorable for foraging because of reduced costs of slower water. Theoretically, foraging in the deeper of two habitats ought to increase a fish's prey encounter rate if water velocity and prey density remain constant. Prey encounter rate should increase with increasing water depth until depth reaches the fish's maximum prey detection distance, after which it should asymptote.

For drift feeders, foraging in deeper, slower, versus shallower, faster water should represent a tradeoff in prey encounter rate, assuming equal stream channel width and equal prey density (Y number of prey $\cdot$ m^{-3}) throughout the water column. This is illustrated by the following:

Assume that the prey encounter rate in a slower, deeper section is $0.5Y$ prey $\cdot$ sec^{-1}, calculated as:

$$[Y \text{ prey} \cdot m^{-3}] \text{ x } [1\text{-m wide x } 1\text{-m deep x } 0.5\text{-m} \cdot sec^{-1}] = 0.5Y \text{ prey} \cdot sec^{-1}$$

Prey encounter rate would be equal in a faster, shallower section, calculated as:

$$[Y \text{ prey} \cdot m^{-3}] \text{ x } [1\text{-m wide x } 0.5\text{-m deep x } 1\text{-m} \cdot sec^{-1}] = 0.5Y \text{ prey} \cdot sec^{-1}$$

The two habitats may differ, however, in the way in which they influence a fish's ability to detect and capture prey. Faster water velocity may reduce the prey detection

area and capture probabilities within this area (Godin and Rangeley 1989, Hill and Grossman 1993, O'Brien and Showalter 1993, Chapter One). The effect of deeper water on prey detection and capture probabilities, however, has never been investigated. Although prey encounter rates might be equal in deeper/slower vs. shallower/faster habitats, prey capture probability is likely to be determined by the fish's ability to forage in these habitats. Bisson et al. (1988), for example, proposed that coho may be better adapted to forage in pools, and steelhead in riffles, based on differences in body form. A better understanding of the influence of water depth on the foraging abilities of stream salmonids should help to explain habitat selection and segregation.

Our objective was to assess the influence of water depth on prey detection and capture by juvenile coho and steelhead. We used three-dimensional video analysis of stream-tank foraging experiments to test these hypotheses: 1) prey capture probability increases with increasing water depth, and 2) there are species-specific differences in capture probability, prey detection distance, prey interception speed, and speed of return to the focal point, that might facilitate foraging in their respective preferred habitats. We also used the relationship between water depth and capture probability to predict the effect of depth on prey capture rates for coho and steelhead.

METHODS

Stream tank

We modified the variable-depth and -velocity stream tank for these experiments (see Chapter One. The experimental arena measured 1.5 m long x 0.6m-wide, and depth treatments were 0.15, 0.30, 0.45, and 0.60 m. Prey were delivered through the upstream screen via any one of 20 plastic feeder tubes (6.25-mm diameter) arranged in four layers of 5 each, equally-spaced in rows at depths 0.15, 0.30, 0.45, and 0.60 m. A series of ten 1000-Watt aquarium heaters was used to maintain constant water temperature (mean = 8.5 °C, SD 1.03).

Experimental protocol

Ten wild fish of each species (50- 60 mm fork length) were collected from Peterson Creek, near Juneau, Alaska in October 2002. All fish were collected from the same stream reach. We conducted our experiments at the University of Alaska Fairbanks Salmon Laboratory, located in the Macaulay Hatchery, Juneau, Alaska. Fish were held in flow-through 40-L circular tanks and fed maintenance rations of frozen brine shrimp. Filtered freshwater was supplied by a subsurface line from Salmon Creek Reservoir, near Juneau, Alaska. Photoperiod was maintained at 18 h day and 6 h night.

We selected four water depth treatments (0.15, 0.30, 0.45, and 0.60 m) that spanned the published range of depth preferences for juvenile coho and steelhead ~60 mm fork length (Everest and Chapman 1972, Sheppard and Johnson 1985, Beecher et al. 2002).

Water velocity was held constant at 0.30 m · sec^{-1} mean column velocity, measured 0.20 m upstream from the fish's focal point. We randomly selected 4 fish of each species, ranging from 53-65 mm fork length, and species-paired by size. Each fish was tested individually at each depth, assigned in a random order with two days rest between treatments. Two pairs of fish were tested each day and the entire series of feeding trials was completed in eight days to minimize any effects of time or growth. Fish were not fed for 24 hours prior to a feeding trial to ensure they would be motivated to feed.

Each fish received a 15-minute "warm-up" feeding trial to acclimate them to the experimental arena. For each feeding trial a fish was netted from its individual raceway and quickly released into the experimental arena. When the fish was observed to be feeding actively, the trial began. A feeding trial consisted of 100 individual prey being fed to a fish over a 25 minute period (4 prey · min^{-1}). Prey were adult brine shrimp cut to 2-mm length to ensure that the fish's reaction distance to the prey would be less than half of the tank width (Dunbrack and Dill 1984). Prey were randomly assigned to one of the 20 feeder locations, and were fed at random times within each 15-sec interval. Prey were fed only through the feeder tubes that were submerged at a respective depth treatment (e.g. 20 per each of 5 tubes at 0.15-m depth, 5 at each of 20 tubes at 0.60-m depth). At the conclusion of the experiment fish were fed extra prey to be sure that they had not become satiated, and they were always observed to eat more prey.

We recorded our feeding trials on miniDV cassettes using two Sony GVD900 tape recorders and two Sony EVI 334 video cameras. Cameras were positioned at ~ 90 degrees from each other relative to the fish focal point to facilitate 3-D analysis.

Data analysis

See Chapter One for a detailed description of the 3-D analysis. Figure 2.1 shows an example of the 3-D data for coho at 0.15 and 0.60 cm.

We used linear regression (Zar 1999) to assess the effect of water depth on prey capture probabilities and feeding performance measures. The following regressions were fitted separately for coho and steelhead: 1) prey capture probability vs. water depth, 2) mean prey detection distance vs. water depth, 3) mean prey interception speed vs. water depth, and 4) mean return speed vs. water depth. We tested for significance of the individual regressions ($\alpha = 0.05$), and compared the slopes and elevations between the species using Student's *t*-tests ($\alpha = 0.05$, two-tailed) to test the null hypotheses that 1) the slopes and 2) and elevations between two regression lines are equal Zar (1999). We also conducted a power analysis to assess our ability to detect differences between the slopes of the regression lines for prey capture probability vs. water depth. We used the *PS* software program, which is designed specifically for assessing power and sample size for comparisons of two linear regressions (Dupont and Plummer 1998).

We held prey encounter rate constant ($4 \cdot \text{min}^{-1}$) across all treatments to minimize the likelihood of an interaction between capture probability and handling time. This means that prey density (number prey per unit volume), however, decreases as depth treatment increases because water volume increases. To account for this we calculated predicted prey capture rate vs. water depth as follows:

[Number of prey caught] x [Treatment depth/0.60]

We plotted the predicted prey capture rate for each fish at each depth, and drew a linear regression line for each species. Because these relationships are derived from the prey capture probability regressions we do not report statistical results for them. These density-corrected relationships provide predictions of how water depth influences prey capture rate by coho and steelhead in natural streams.

We also plotted prey capture probability by 0.15-m horizontal depth layer and by 0.12-m vertical columns within each depth treatment to provide a graphical description of how depth influenced probability within the foraging area.

RESULTS

Prey capture probability

The relationship between prey capture probability and water depth was not significant for either coho ($P = 0.50$, $r^2 = 0.03$) or steelhead ($P = 0.98$, $r^2 < 0.01$) (Table 2.1. Fig. 2.2A). The slopes of the regression lines did not differ significantly ($P = 0.61$), but the elevations did ($P = 0.03$), with coho averaging greater capture probabilities across all depths (Table 2.1. Fig. 2.2A). Power analysis showed that we had only 5.2% power ($\alpha = 0.05$) of correctly rejecting the null hypotheses that the regression slopes or elevations for coho and steelhead were equal, however, if the observed differences between these slopes and elevations were real.

When we corrected for prey density, we found a positive linear relationship between predicted prey capture rate and increasing water depth (Fig. 2.2B). We did not see the expected asymptote of prey capture rate vs. depth for either species.

3-D analysis: prey detection, capture, and return to the focal point

We found a significant linear increase in prey detection distance with increasing water depth for coho ($P < 0.001$, $r^2 = 0.88$) and steelhead ($P < 0.001$, $r^2 = 0.69$) (Table 2.1. Fig. 2.3A). Neither the slopes nor the elevations of the regression lines differed significantly (Table 2.1, Fig. 2.3A). Prey were detected throughout the reaction volume rather than on the surface at maximum detection distance. Mean prey detection locations for both species were further upstream in deeper water (Fig. 2.4).

We also found a significant linear increase in prey interception speed with increasing water depth for coho ($P < 0.05$, $r^2 = 0.32$) and steelhead ($P < 0.05$, $r^2 = 0.37$) (Table 2.1. Fig. 2.3B). Neither the slopes nor the elevations of the regression lines differed significantly (Table 2.1, Fig. 2.3B). Because fish swam faster to cover the increased detection distance, the mean downstream (x-axis) capture location changed little with increasing water depth (Fig. 2.4). At 0.15 and 0.30 m depths fish swam slower than their predicted maximum sustainable swimming speeds (Vmax, 0.33 m · sec^{-1}, as calculated using equations for juvenile sockeye salmon of the same size (Brett and Glass 1973)). At 0.60 m depth they swam faster than Vmax (Fig. 2.3B).

Prey capture probabilities by 0.15-m depth layer within depth treatments were always lower in the surface layer (Fig. 2.5). In deeper treatments probabilities were greater near the substrate, and they dropped off in the surface layers, particularly at the lateral edges (Figs. 2.5 and 2.6).

The speed of return to the focal point was not significantly related to water depth for coho ($P = 0.23$, $r^2 = 0.10$) or steelhead ($P = 0.95$, $r^2 < 0.01$) (Table 2.1. Fig. 2.3C). The slopes of the regression lines did not differ significantly ($P = 0.37$), but the elevations lines did ($P < 0.001$) with steelhead retuning at slightly faster speeds across all depths (Table 2.1, Fig. 2.3C). Fish returned to the focal point at approximately Vmax at all depths (Fig. 2.3C).

DISCUSSION

We found little relationship between water depth and prey capture probability for either coho or steelhead. With increasing depth, capture probability for coho increased only 6.2%, whereas probability for steelhead changed little (< 1%). This suggests that any benefit of foraging in deeper water would be due more to an increase in prey encounter rate (i.e. greater volume searched) than to a physical response to foraging in deeper water (e.g. an increase prey detection probability). For example, the observed increase in prey detection distance in deeper water for both coho and steelhead might be expected to lead to an increase in prey detection and capture probabilities. The fact that we did not see this, however, suggests that the benefits of increased prey detection distance in deeper water may be countered by a reduction in search efficiency within a greater volume of water. This is supported by our finding of increased capture probabilities near the focal point in conjunction with low probabilities in the surface layers in the deeper treatments (Figs. 2.5 and 2.6). Our finding from Chapter One, that an increase in search volume in faster water also decreased capture probabilities, further supports the idea that search efficiency decreases as search volume increases.

Although capture probabilities did not increase in deeper water, predicted capture rates did increase. Because capture probabilities were constant across all depths, prey capture rate increased proportionally to depth. The relationship between prey capture rate and water depth, therefore, is additive; i.e. assuming equal water velocities and prey densities, each increase in depth adds more potential prey without a loss or gain in overall

capture probability. We used relatively small fish and deep water, but we were unable to demonstrate the asymptote in capture rate that we predicted would occur at depths beyond the fishes' maximum prey detection distance. Our fish (~60 mm) are predicted to have a reaction distance of ≤ 0.80 m for the size of prey we used (Dunbrack and Dill 1983), and the maximum prey detection distance in our 0.60 m depth treatment (0.79 m) closely agrees with this. Because our fish detected some prey almost directly overhead, an asymptote in prey capture rate might not be seen until depths of > 0.80 m for fish of this size. To maximize prey capture rate, therefore, fish should select the deepest water available up to their maximum prey detection distance, assuming equal velocity and prey density (other factors, such as predation risk, notwithstanding).

Water depth is one of the most commonly reported habitat descriptors for coho and steelhead (Bugert et al. 1991, Beecher et al. 1995, Beecher et al. 2002) and for stream salmonids in general (Everest and Chapman 1972, Greenberg et al. 2001, Heggenes 2002, Polacek and James 2003). The value of deeper water has been attributed to increased survival by providing cover (Bustard and Narver 1975, Gibson and Power 1975, Kruzic et al. 2001) and to foraging benefits because of reduced prey capture costs (Rosenfeld and Boss 2001, Young 2004). Our results show that increased prey capture rate may also be an important factor in depth selection.

We hypothesized that at least one species would display significantly better foraging capabilities in their respective preferred habitat (i.e. coho in deeper or steelhead in shallower water). The similar response to water depth by both species, however, mirrors our findings on the effects of water velocity, and it strengthens the evidence that both

species are equally capable of exploiting a wide range of habitats. The fact that the age classes (and mean sizes) of fish differed between the experiments suggests that these equal foraging capabilities continue through time. Despite the widely-cited pattern of stream habitat segregation of coho in pools and steelhead in riffles (Hartman 1965, Bugert et al. 1991) both species are also successful in rearing in lakes or ponds (Swain and Holtby 1989, Behnke 1992, Irvine and Johnston 1992, Hayes 1995) where they cruise feed for zooplankton, small fish, or aerial invertebrates. It is apparent that a considerable amount of flexibility in foraging behavior is maintained within the genomes of both coho and steelhead (e.g. Dill 1983).

Comparing maneuver characteristics between our depth and velocity experiments provides further evidence of the flexibility of coho and steelhead foraging behavior. In the depth experiments prey detection distance and interception speed increased, and return speed remained constant, with increasing water depth. Conversely, in response to increasing water velocity interception speed remained constant and return speed increased (Chapter One). This suggests that juvenile salmonids are capable of adjusting to changes in their foraging environment to a remarkable degree. In each case the fish were presented with the same problem, capturing a prey and returning to their focal point, but under different environmental gradients (either slow-fast or shallow-deep). In the velocity experiments, where detection distance declined at faster velocities, they did this by maintaining the same interception speed and increasing their return speed. In the depth experiments, where they had the opportunity to detect prey at increasing greater distances, they increased their interception speed, and held return speed constant

Fish size also plays a role in stream salmonid habitat selection and segregation, because fish move into faster deeper water as they grow (Lister and Genoe 1970, Everest and Chapman 1972). We found that the smaller fish used in the depth experiments (~60 mm) had lower prey capture probabilities than did larger fish (~ 80 mm, Chapter One) when tested at the same depth and velocity. At 0.30-m depth and 0.30 m · sec^{-1} velocity, mean capture probabilities were 48% for the smaller fish and 65% for the larger fish (17% difference), whereas differences between species were 11% and <1% for the small and large classes, respectively. Fish size, therefore, appears to have a greater influence on prey capture ability than does species. Hartman (1965) hypothesized that competition between coho and steelhead was minimized by differences in body size due to earlier emergence of coho. Although he documented that steelhead grow faster than do coho, he noted that coho emigrated as smolts early in their second year, thus avoiding potential competition during the second summer when fish of both species would be of equal size. In the northern end of their distributions, coho and steelhead spend this second summer in sympatry, and they are often of equal size during this period (Groot and Margolis 1991, Lohr and Bryant 1999, Halupka et al. 2000). There are no published accounts of habitat selection in natural streams by equal-sized coho and steelhead in sympatry so it is currently unknown whether segregation is based on differences in habitat preferences or simply on fish size.

Differences in the elevations, but not in the slopes, of the regression lines show that coho had an equal advantage in prey capture probability among all depth treatments. Although this difference did not appear to be related to water depth (i.e. the slopes of the

lines did not differ), it is of some interest. One possible explanation is that the coho were more experienced foragers than were the steelhead, having spent up to two months more time foraging in the wild before they were collected in October. In the velocity experiments (Chapter One), in which we used older fish (age I+) which had spent over a year foraging in the wild, we did not find a systematic species difference. It is possible that the greater relative difference in experience between age 0+ fish gives coho an advantage, but that by their second summer both species have enough experience to render the difference unimportant.

It is also possible that the non-significant differences between coho and steelhead in the slopes of prey capture probability vs. depth represent a true advantage for coho in deeper water. Statistical power for this comparison was low, and the relatively high variation may have masked the treatment effects. There is an indication that coho had greater capture probabilities near the surface in the deeper treatments. This led to the slight increase in the slope of capture probability for coho. Whether this is a true species difference, or one due to age-based differences in experience as discussed in the previous paragraph, remains to be determined. Clearly, our predicted relationships between water depth and prey capture rate need to be viewed as models that need further experimental confirmation.

This study demonstrates that foraging in deeper water may increase prey capture rate for drift-feeding juvenile salmonids. Deeper water, however, may also convey other costs or benefits. Deeper water may provide cover from aerial or surface feeding predators such as kingfishers or mergansers (Bugert and Bjornn 1991, Gregory 1993,

Grand and Dill 1997); conversely, it may increase predation risk from aquatic predators such as larger fish (Bugert and Bjornn 1991, Gregory 1993). Deeper water can provide shelter from high flows, one reason pools are often cited as critical overwinter habitat (Bustard and Narver 1975, Maeki-Petaeys et al. 2000, Solazzi et al. 2000). The results of our foraging experiments need to be considered in light of these larger concerns, but they offer increased insight into the complex association between stream salmonid distribution and physical habitat.

CONCLUSIONS

We found little relationship between prey capture probability and water depth for coho and steelhead, but predicted prey capture rates increased with increasing depth. This leads us to conclude that any benefits of foraging in deeper water are more likely due to increased prey encounter rate than to increased capture probability. We did not find a significant difference in prey capture probabilities between coho and steelhead, but statistical power was low. Prey capture maneuver characteristics were very similar between the species. These included positive relationships between water depth and 1) prey detection distance, and 2) interception speed. Return speed was constant across all depths. In the deeper treatments, coho had greater capture probabilities nearer the surface than did steelhead, but it is unclear if this was a species difference or one based on the relative amount of foraging experience fish had in the wild prior to capture. We conclude that foraging in deeper water may increase prey capture rates for coho and steelhead, but that further experimental work is needed.

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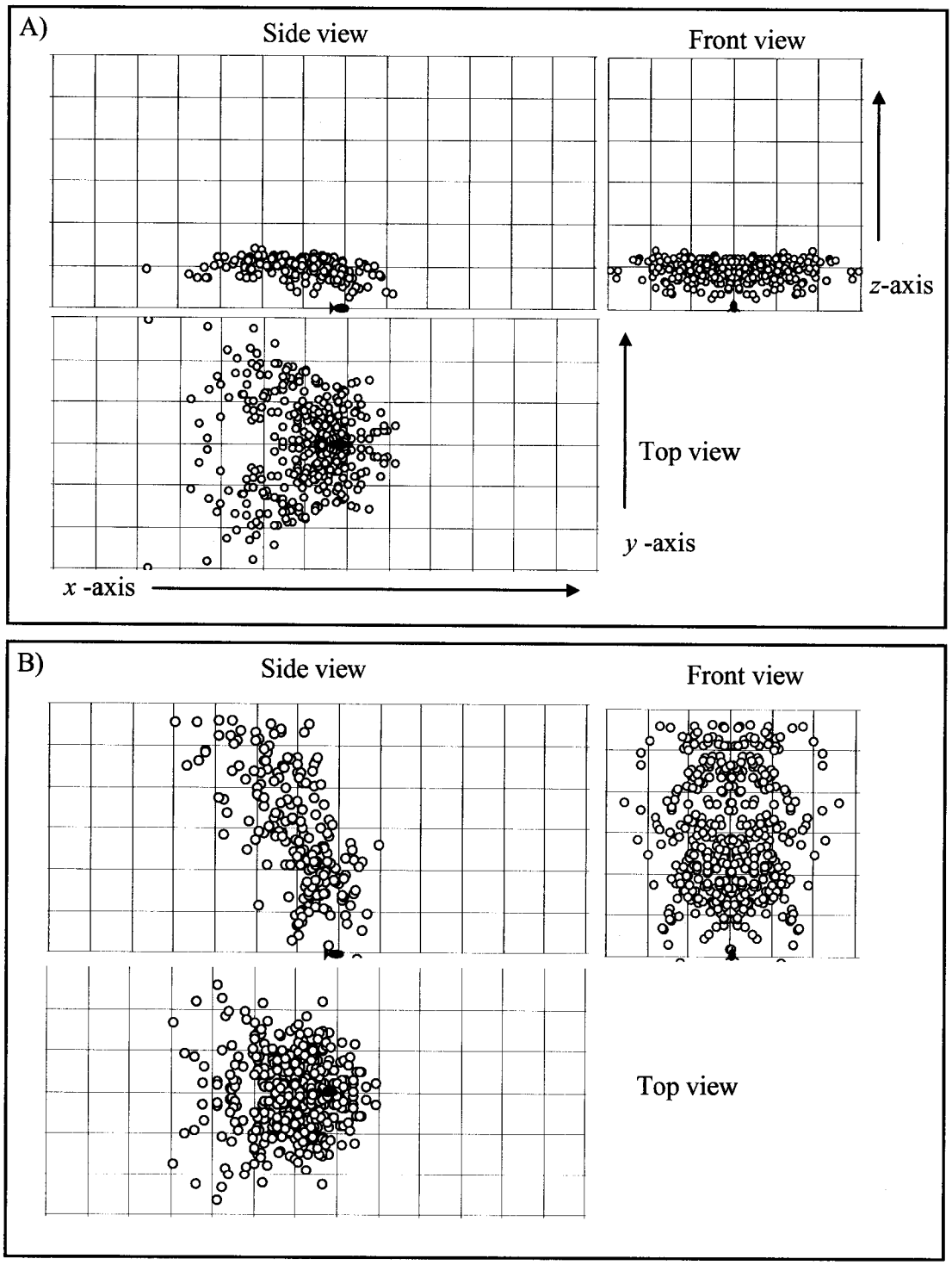

Figure 2.1. Capture locations in three dimensions for coho ($N = 4$) at two depth treatments, A) 0.15 m, and B) 0.60 m. Each circle represents the *x,y,z* coordinates of a prey capture. Grid squares are 0.1 x 0.1 m.

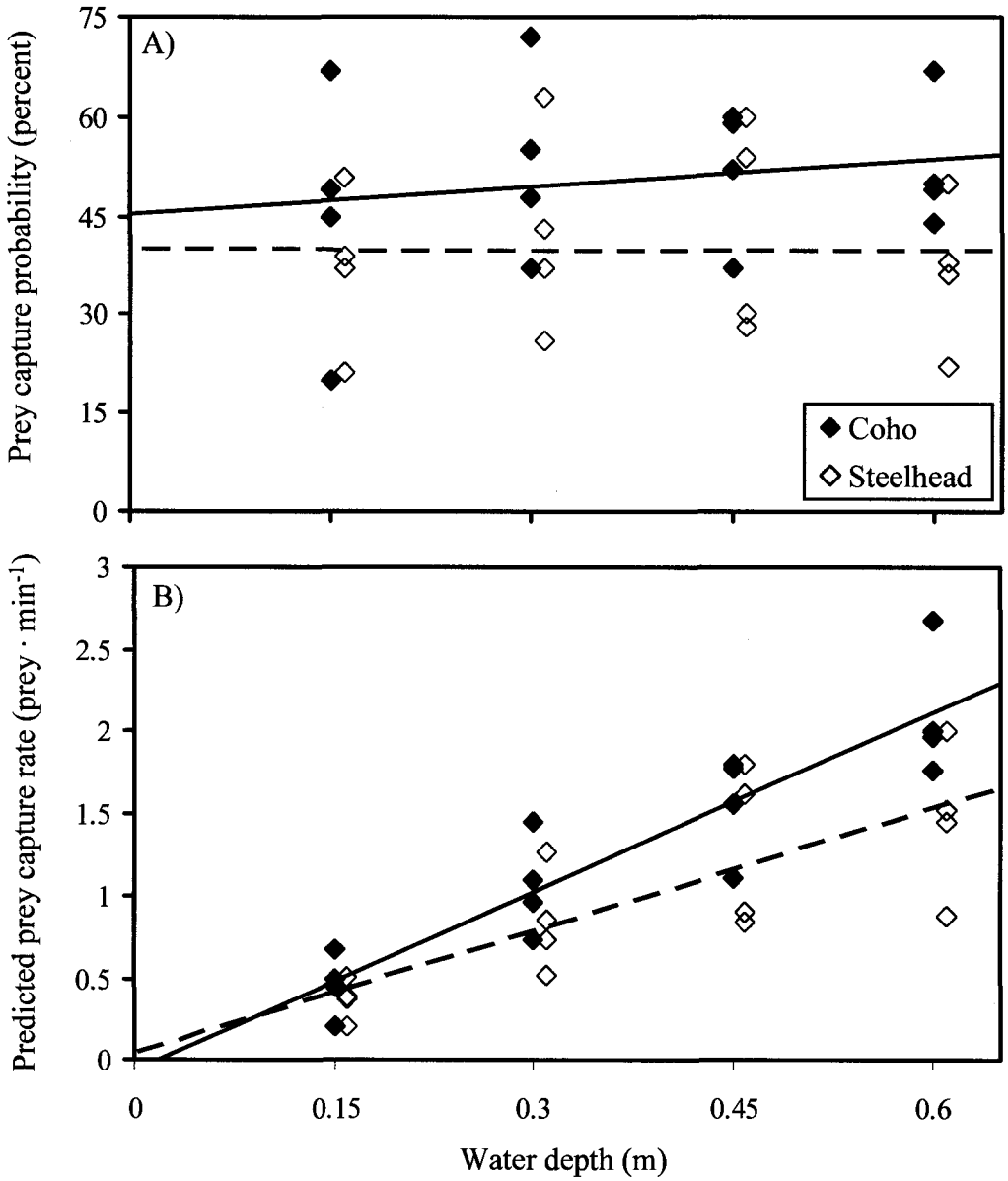

Figure 2.2. A) Prey capture probability, and B) predicted prey capture rate, vs. water depth for coho (solid diamonds and lines) and steelhead (open diamonds, dashed lines). Regression equations and significance tests are found in Table 2.1. Each data point represents the probability or rate for one fish (n = 4 of each species). Steelhead data points are offset by +0.01 m for visual clarity.

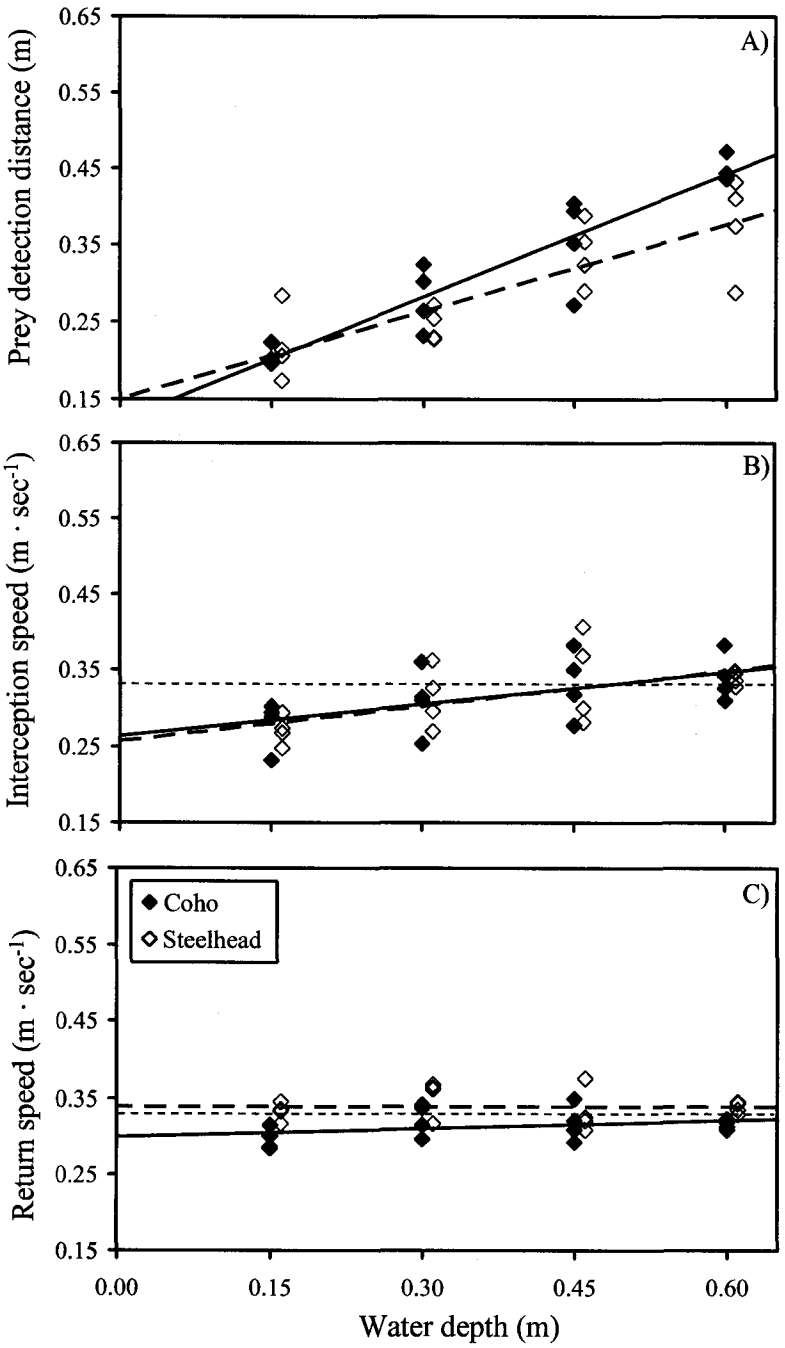

Figure 2.3. Mean: A) prey detection distance, B) interception speed, and C) return speed, vs. water depth for coho (solid diamonds and lines) and steelhead (open diamonds, dashed lines). Regression equations and significance tests are found in Table 2.1. Each data point represents the mean value of the *y* variable for one fish. The finely-dashed horizontal lines in panels B) and C) are the predicted maximum sustainable swimming speeds for coho and steelhead. Steelhead data points are offset +0.01 m for visual clarity.

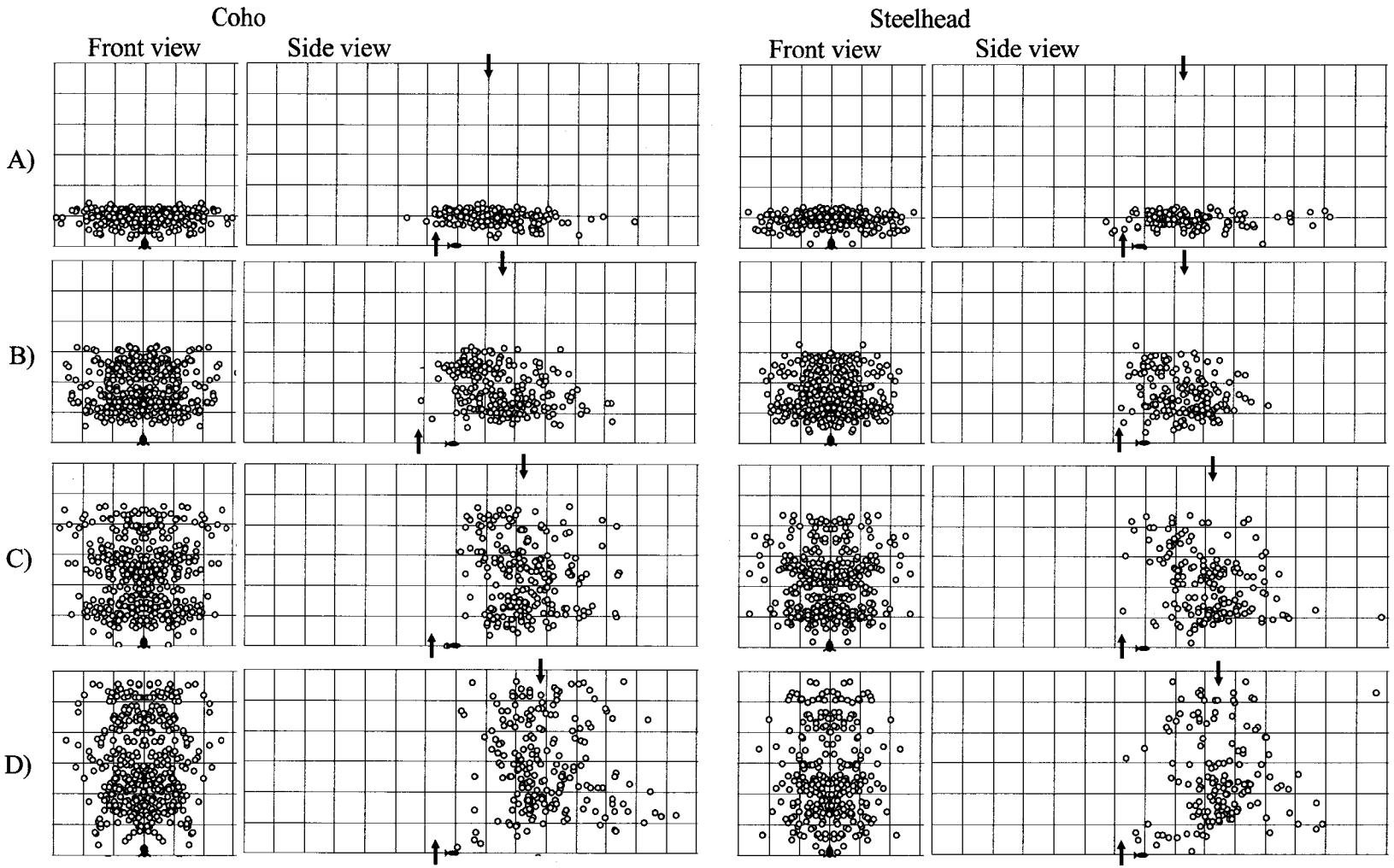

Figure 2.4. Front and side view of prey detection locations for coho (left) and steelhead (right) at depths (m) of A) 0.15, B) 0.30, C) 0.45, and D) 0.60. Data are pooled for all fish at each treatment (n = 4 of each species). Arrows indicate mean *x*-axis distances for prey detection (pointing downward) and prey capture (pointing upward). Grid squares are 0.10 x 0.10 m.

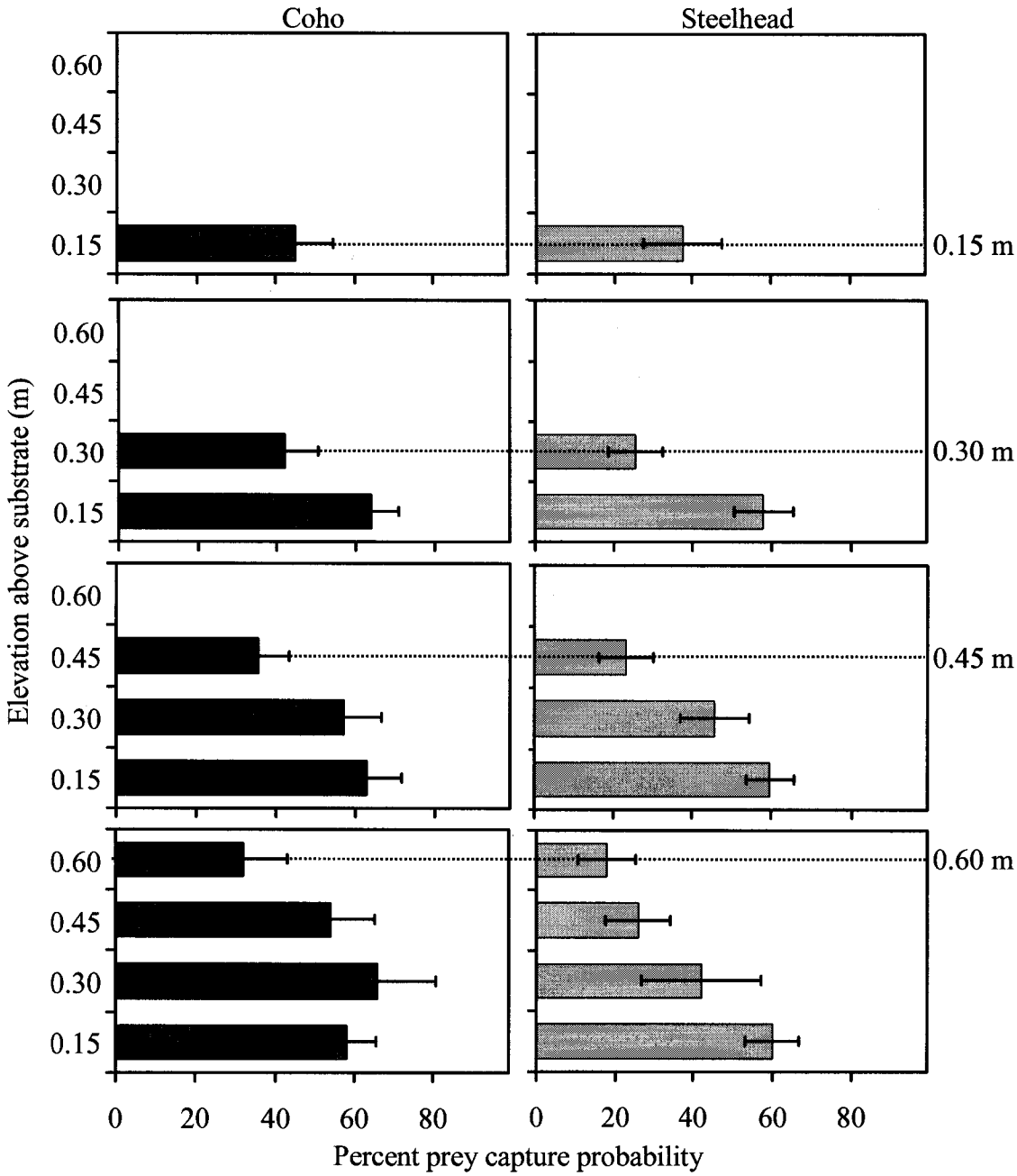

Figure 2.5. Prey capture probability vs. elevation above the substrate by depth layer within treatments for coho (left, darkly shaded bars) and steelhead (right, lightly shaded bars). Each bar represents the mean of four fish for each species. Error bars are +/- 1 SE. Depth treatment levels are 0.15, 0.30, 0.45, 0.60 m, top to bottom. Horizontal dotted line in each graph shows elevation above the substrate of the water surface.

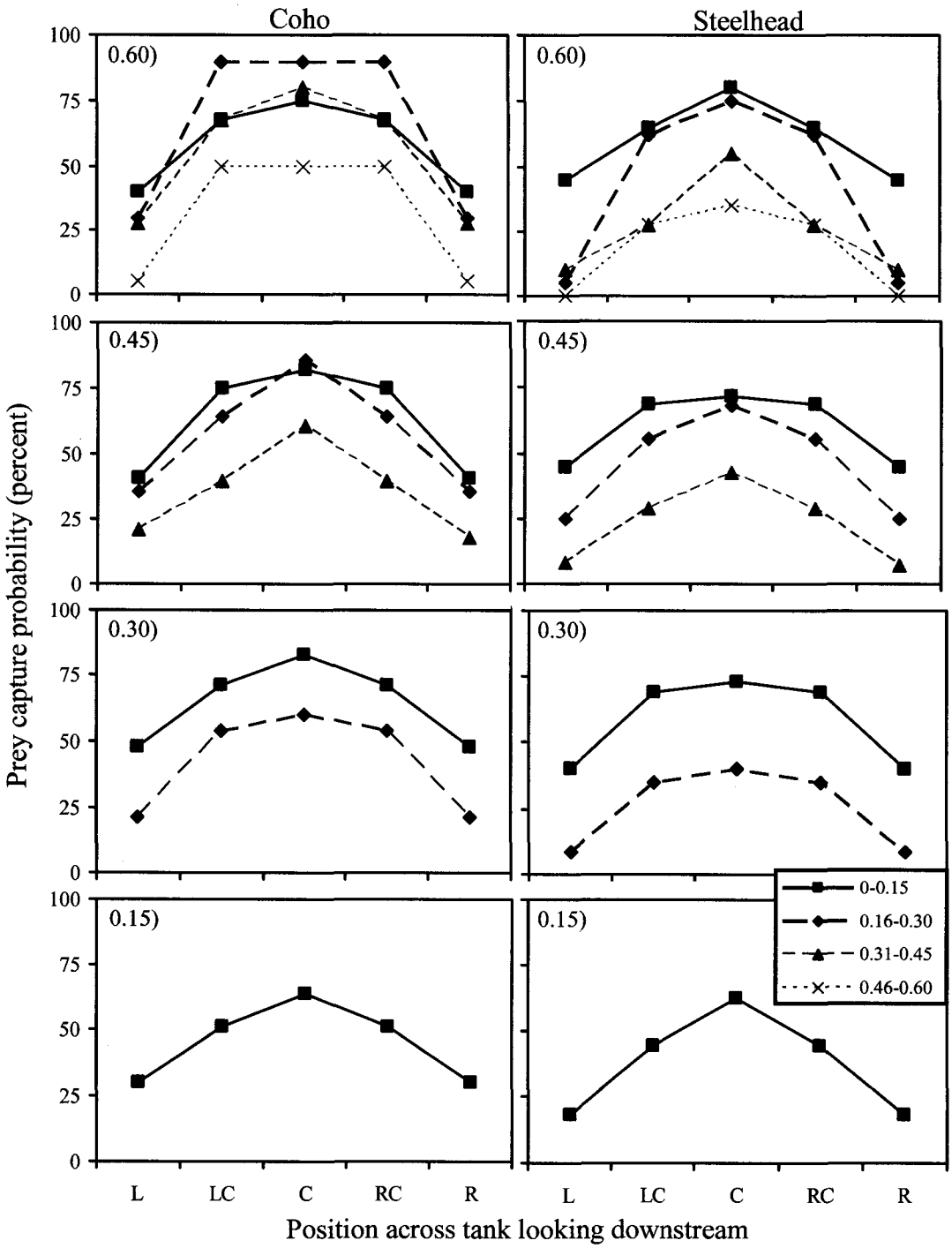

Figure 2.6. Prey capture probabilities for coho (left) and steelhead (right) vs. lateral position across the stream tank, by 0.15-m depth layers within depth treatment levels. Lateral positions are in 0.12 m increments looking downstream (L = 0-0.12, LC = 0.13-0.24, C = 0.25-0.36, RC = 0.37-0.48, R = 0.49-0.60). Depth treatments (m) are in the upper left of each graph, and depth layers (m) are identified in the legend.

Table 2.1. Regression equations and significance tests for prey capture characteristics of juvenile coho salmon and steelhead ($N = 4$). Regression x variable in all equations is water depth (m). F values are for significance of individual species' regressions (* = $P < 0.05$, ** = $P < 0.001$). t values are for significance tests -tests indicate failure to reject the null hypothesis that the slopes or the elevations of species' regression lines are equal (Zar 1999).

Regression y variable	Regression equation	r^2	F value	t value for test for equal slopes	t value for test for equal elevations
Number of prey captures					
Coho	$y = 13.8x + 45.5$	0.03	0.49	0.51	2.36
Steelhead	$y = -0.05x + 39.9$	<0.01	<0.01		
Prey detection distance (m)					
Coho	$y = 0.53x + 0.12$	0.88	103.53**	1.88	1.81
Steelhead	$y = 0.37x + 0.15$	0.69	31.53**		
Interception speed ($m \cdot sec^{-1}$)					
Coho	$y = 0.14x + 0.26$	0.32	6.64*	0.19	0.05
Steelhead	$y = 0.15x + 0.26$	0.37	8.12*		
Return speed ($m \cdot sec^{-1}$)					
Coho	$y = 0.04x + 0.30$	0.10	1.61	0.91	3.72
Steelhead	$y = -0.002x + 0.34$	<0.01	<0.01		

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Appendix 2.1. Results of experiments on the effect of water depth on juvenile coho and steelhead. Number of prey captures are the results of each fish at each depth (n = 4 for each species). Mean values are for multiple observations of detection distance and interception and return speed for each fish.

Water depth (m)	Number of prey captures		Mean Prey detection distance (m)		Prey interception speed ($m \cdot sec^{-1}$)		Speed of return to focal point ($m \cdot sec^{-1}$)	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
15	20	21	0.20	0.21	0.29	0.30	0.30	0.34
15	45	39	0.26	0.23	0.31	0.36	0.34	0.32
15	67	51	0.35	0.39	0.35	0.41	0.35	0.32
15	49	37	0.44	0.29	0.33	0.34	0.32	0.34
30	37	26	0.20	0.17	0.30	0.27	0.29	0.32
30	55	43	0.32	0.27	0.36	0.33	0.34	0.37
30	48	37	0.40	0.32	0.38	0.30	0.32	0.38
30	72	63	0.44	0.41	0.38	0.35	0.31	0.33
45	37	30	0.22	0.28	0.29	0.27	0.29	0.34
45	60	60	0.30	0.25	0.31	0.30	0.30	0.36
45	52	28	0.39	0.35	0.32	0.37	0.31	0.32
45	59	54	0.47	0.43	0.34	0.35	0.31	0.34
60	49	22	0.20	0.21	0.23	0.25	0.32	0.33
60	50	38	0.23	0.23	0.25	0.27	0.32	0.36
60	44	36	0.27	0.29	0.28	0.28	0.29	0.31
60	67	50	0.44	0.37	0.31	0.33	0.32	0.35

CHAPTER THREE

CAN VELOCITY-DEPENDENT DIFFERENCES IN NET ENERGY INTAKE RATES EXPLAIN HABITAT SEGREGATION BETWEEN JUVENILE COHO SALMON AND STEELHEAD?[1]

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Abstract. We developed models to predict the effect of water velocity on prey capture rates and on optimal foraging velocities of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*). Mean size of both species was ~ 80 mm, the size of age I+ coho and steelhead during their second summer in Southeast Alaska streams, when size overlap suggests that competition might be strongest. We used experimentally-determined relationships between prey capture probabilities and water velocity to predict gross energy intake and prey capture costs, and we used the difference of these to predict velocities at which each species maximized net energy intake. Optimum velocity was 0.29 $m \cdot s^{-1}$ for coho and 0.30 $m \cdot s^{-1}$ for steelhead. Because coho are assumed to pay a greater swimming cost due to a less hydrodynamic body form, we also modeled 10% and 25% increases in prey capture costs for coho, which reduced optimum velocity by 0 and 0.01 $m \cdot sec^{-1}$, respectively. We conclude that velocity-dependent constraints on prey capture ability are more important than are prey capture costs in determining optimum velocities. Because experimental results have shown that these constraints are similar for coho and steelhead, we suggest that water velocity is not the primary niche axis upon which the species segregate stream habitat.

INTRODUCTION

Differences in foraging abilities between closely-related fish species have been shown to reduce niche overlap (Werner 1977), a central explanation for habitat segregation and species coexistence in ecology (Schoener 1974). In this paper we test the hypothesis that two sympatric stream salmonids, juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*), have different optimal foraging velocities, thus reducing niche overlap and facilitating coexistence through habitat segregation. Coho and steelhead have been shown to segregate stream habitat, with coho using slower, deeper pools and steelhead using faster, shallower riffles (Hartman 1965, Allee 1981, Bisson et al. 1988, Bugert et al. 1991). Explanations for this have included both of Nilsson's (1967) proposed mechanisms for species segregation: 1) interactive segregation, whereby one species displaces the other from a preferred habitat (Hartman 1965, Young 2004), and 2) selective segregation, whereby the species select their respective habitats based on differential abilities to forage there (Fraser 1969, Allee 1974, Bugert and Bjornn 1991). Foraging ecology has been a focus of research on coho and steelhead habitat segregation (Hartman 1965, Fraser 1969, Allee 1974, Sheppard and Johnson 1985, Bisson et al. 1988, Harvey and Nakamoto 1996, Young 2001, Young 2004); although it is widely assumed that the species either compete for, or select, energetically-favorable foraging habitats, no study has addressed how water velocity influences the energetic costs and benefits of foraging for coho and steelhead.

Cost-benefit analyses have played a central role in the development of foraging- and habitat-selection theory in ecology (Holling 1959, MacArthur and Pianka 1966, Charnov 1976, Stephens and Krebs 1986). For drift-feeding salmonids, the metabolic cost of foraging against a current is balanced against the benefit of more prey encounters in faster water (Everest and Chapman 1972, Wankowski 1981). The velocity at which a fish can maximize its net energy intake (NEI) rate, therefore, is determined by the relative magnitude of its costs vs. benefits; it follows that two co-evolved sympatric species might reduce niche overlap by maximizing NEI at different water velocities.

Bisson et al. (1988) suggested that habitat segregation by coho and steelhead might be due to morphology-dependent differences in foraging abilities; coho are more laterally compressed with taller fins, and steelhead are more cylindrical with shorter fins. This would allow coho to forage more efficiently in slower water, where fast turning and acceleration abilities are favored because prey are more patchily distributed. The steelhead body form would be better adapted for to minimize drag while drift-feeding in flowing water. Differences in morphology have been shown to influence feeding performance, competitive ability, and habitat selection in sunfish (Werner 1977, Huckins 1997) and sticklebacks (Lavin and McPhail 1986), but this idea has not been tested for two sympatric stream salmonids.

Our objective was to develop models that predict optimum foraging velocities for coho and steelhead using the results of our experiments on the effects of water velocity (Chapter One). To do this, we modeled gross energy intake and capture costs, and estimated NEI as the difference between these curves. We use NEI to predict optimum

foraging velocities, to test the hypothesis that coho have a slower optimum velocity than do steelhead. We also assessed how 10% and 25% increases in foraging costs for coho (as suggested by body form) influence NEI rate and optimal foraging velocity.

METHODS

The methods for the foraging experiments that we used to predict the effect of water velocity on feeding performance of coho and steelhead are described in Chapter One. We used the linear regressions of prey capture probabilities vs. water velocity (Fig. 3.1 A) to predict prey capture rates for coho and steelhead (Fig. 3.1 B). To do this we need to account for differences in prey density among velocity treatments. This is done as follows:

For the foraging experiments we held prey encounter rate constant (4 prey $\cdot$ min^{-1}) across all velocity treatments to minimize the possibility of an interaction between water velocity and prey handling time. This resulted in a decrease in prey density (number of prey $\cdot$ m^{-3}) as velocity increased, because the volume of water increased while the number of prey was constant. In streams, prey encounter rates are expected to increase proportionally with water velocity (Everest and Chapman 1972, Wankowski and Thorpe 1979). To correct for prey density, we predict prey capture rate as follows:

Prey capture rate = [Number of prey captured] x [Treatment velocity/Fastest velocity]

This gives the number of prey per 25-minute feeding trial, which is then multiplied by 2.4 to predict number of prey per hour.

We plotted density-corrected prey capture rate vs. water velocity for all fish from the foraging experiments. We then plotted density-corrected capture curves for each species by predicting capture rate at 0.01-m intervals using the regression equations from Chapter One:

For coho: $y = -169.2x + 112.0$

For steelhead: $y = -151.9x + 104.8$

Where y = the number of prey captured and x = water velocity ($m \cdot sec^{-1}$).

We predicted GEI ($j \cdot hr^{-1}$) versus water velocity for each species by substituting the mean energy content of a 2-mm mayfly (Cummins and Wuycheck 1971) for that of our 2-mm brine shrimp. The cut brine shrimp were not dissimilar in size or shape to a 2-mm mayfly.

To estimate NEI we used the following model:

$$NEI = GEI - EC$$

Where EC is the energetic cost ($j \cdot hr^{-1}$) of prey capture, including search costs (SC) and handling costs (HC). Energetic costs are therefore:

$$EC = [(ST \cdot SC) + (HT \cdot HC)]$$

Where search time (ST) is the time spent at the focal point and handling time (HT) is the time spent pursuing prey and returning to the focal point. We designated the median search time for each species at each velocity as the total time (TT) of the experiment minus the sum of the median interception time (IT) plus the median return time (RT):

$$ST = TT - (IT + RT)$$

We estimated the cost of search time as steady swimming, using the temperature-, size-, and swimming speed-specific metabolic rates (mg $O_2 \cdot kg^{-1} \cdot hr^{-1}$) developed by Brett and Glass (1973) for juvenile sockeye salmon. We used this rate for both species because it is the only relationship developed for juvenile salmon that covers the fish sizes, temperatures, and swimming speeds we used. Puckett and Dill (1985) reported that metabolic rates for sustained swimming in coho (40 mm, 15° C) closely matched those of sockeye under similar conditions, and that the sockeye relationship could be used for coho. Morgan and Iwama (1991) reported that metabolic rates for juvenile steelhead were comparable to those reported by Brett and Glass (1973) for sockeye of similar size and activity.

We estimated the costs of prey interception and return as unsteady swimming costs, based on a model developed by Hughes and Dill (in prep.). The model estimates costs of unsteady swimming by multiplying steady-swimming costs by a drag multiplier to simulate the cost of swimming associated with prey capture maneuvers.

We predicted the optimum foraging velocity for each species as the velocity at which NEI peaked. We also assessed the effects of increased prey capture costs on optimal velocity for coho by modeling 10% and 25 % increases in the drag multiplier for both steady and unsteady swimming costs.

RESULTS

Predicted prey capture rates peaked at 73 and 71 prey · h^{-1} for coho and steelhead, respectively (Fig. 3.1B). These peaks were the same across a range of velocities of 0.31-0.35 m · s^{-1} for coho and 0.32-0.37 m · s^{-1} for steelhead. Fish could attain 95% of their peak prey capture rates at velocity ranges from 0.25-0.40 and 0.26-0.42 m · s^{-1} for coho and steelhead, respectively. Predicted gross energy intake rate peaked at 70.0 j · h^{-1} (0.33 m · s^{-1}) for coho, and at 68.4 j · h^{-1} (34 m · s^{-1}) for steelhead (Fig. 3.2).

Predicted optimum foraging velocity was 0.29 m · s^{-1} (NEI = 51.2 j · h^{-1}) for coho and 0.30 m · s^{-1} (NEI = 50.4 j · h^{-1}) for steelhead (Fig. 3.2). The ranges where each species could obtain 95% of NEI were 0.24-0.34 and 0.25-0.36 m · s^{-1} for coho and steelhead respectively.

Predicted prey capture costs were similar for coho and steelhead (Fig. 3.2) ranging from ~ 6 j · h^{-1} at slow velocities (i.e. basal metabolic rate) to ~40 j · h^{-1}. At optimum foraging velocities costs were 16.8 and 17. 9 j · h^{-1} for coho and steelhead, respectively, which equals ~25% of GEI for each species. Predicted costs rose exponentially vs. water velocity until they reached the velocity at which they crossed the GEI line. After this they declined sharply because fish were pursuing few prey, so costs were essentially only steady swimming costs at the focal points. Because we used the same equations to predict basal metabolic rates for both species, we would have needed to see differences between the species in the proportion of time spent at the focal point (i.e. steady, slow

swimming) versus that of intercepting prey (unsteady, fast swimming) to see different cost curves. These proportions were, in fact, very similar between coho and steelhead.

Increasing the drag multiplier by 10% and 25% to model increases in prey capture costs for coho decreased optimal velocity by 0 and 0.01 $m \cdot s^{-1}$, respectively (Fig. 3.3).

DISCUSSION

Coho and steelhead differed little in their predicted optimum foraging velocity, and modeled increases in prey capture costs for coho resulted in little decrease in optimal velocities. This suggests that optimum velocities are determined more by constraints on capture abilities than they are by capture costs. These constraints are similar for coho and steelhead (Chapter One), so it is appears unlikely that differences in foraging abilities (i.e. Bisson et al. 1988) are responsible for velocity segregation between the species. Depth-dependent differences in foraging abilities also appear unlikely to explain habitat segregation (Chapter Two). We hypothesize that segregation is either interactive, based on competitive exclusion (Hartman 1965, Young 2004), or selective, based on differences in energetic requirements between the species. The latter include differences in growth requirements based on different age and size of smolting, as has been shown for different life-history types of Atlantic salmon (Thorpe et al. 1998). The mechanism of segregation may also vary temporally and spatially, mediated by environmental factors such as periods of prey limitation. Nakano et al. (1999), for example, demonstrated that coexistence of two species of Japanese charr was facilitated by a foraging-mode shift from drifting to benthic prey during periods of prey limitations. There is limited evidence for prey specialization by coho and steelhead, based on diet composition (Johnston 1970, Johnson and Ringler 1980), but no behavioral studies or experiments have been done.

Laboratory studies have either documented (Hartman 1965) or implied (Young 2001, Young 2004) interactive segregation by coho and steelhead. Hartman found that coho fry (age 0+) were more aggressive than were steelhead fry (age 0+) in pools, whereas steelhead were more aggressive in riffles. He proposed that these behavioral differences might explain his observed pattern of habitat segregation in streams, but he did not test this hypothesis. Young (2001) found that growth of coho and steelhead fry (age 0+) was greatest in laboratory habitats with a mix of pool and riffle habitat (versus either pool or riffle), and he proposed that this was due to reduced competition for space. He also reported that coho excluded steelhead from pool habitat in laboratory streams (Young 2004), although he did not document interactive behavior in these experiments. Because observational field studies that document habitat use and behavior of coho and steelhead in sympatry are lacking, it is unclear if segregation in streams is interactive or selective.

Everest and Chapman (1972) used underwater observation to document velocity selection by juvenile steelhead and Chinook salmon in Idaho streams. They found that habitat segregation was selective and size-based, with fish of each species selecting the same habitats in either allopatry or sympatry. The mean size of fish of each age class differed between the species throughout their period of stream residence, however, thus minimizing interspecific interactions. This is similar to findings for sympatric Atlantic salmon and brown trout (Heggenes 2002), although interspecific interactions are likely to be important at certain spatial or temporal scales (e.g., small streams, low prey availabilities) when sizes overlap (Heggenes et al. 1999).

Most of the published research on coho and steelhead habitat segregation has been conducted in the Pacific Northwest and British Columbia, where there is little size overlap between age 0+ coho and steelhead due to differences in emergence times (Hartman 1965, Fraser, 1969, Allee 1974, Young 2004). In these systems coho usually smolt the following spring, thus avoiding potential competition when sizes overlap. In Southeast Alaska, however, coho remain in streams for a second growing season and smolt at age II+; steelhead remain for at least a third summer and smolt at age III+ (Lohr and Bryant 1999, Halupka et al. 2000). Because steelhead grow faster than do coho, fish of both species are the same size during their second summer at age I+. This is the period during which habitat overlap and competition would be most expected, but there are no published studies of sympatric habitat use for this life stage.

We have observed instances in two separate streams in which age I+ steelhead were actively foraging during the day, while age I+ coho were congregated in deep pools and foraging very little (Piccolo, unpublished data). Age 0+ coho were foraging in close proximity to the age I+ steelhead in both instances, which suggests that the age I+ coho may have chosen not to forage. It is possible that growth requirements of age I+ coho and steelhead differ, and that age I+ coho accept a slower growth rate in exchange for less predation risk because they will smolt early the following summer. This has been suggested for coho (Reinhardt 1999) and clearly demonstrated for Atlantic salmon (Thorpe et al. 1992, Metcalfe 1998, Thorpe et al. 1998, Juanes et al. 2000). If this is the case it would be an example of selective segregation based on long-term survival, rather

than on short-term energetic, considerations. The temporal and spatial persistence of the pattern is undocumented.

Young (2004) proposed that coho competitively excluded steelhead from what he termed mutually preferred, energetically-favorable pool habitat, but he did not document this is natural streams. Our NEI model, however, predicts that optimal foraging velocities for both species are similar, and that NEI peaks at relatively fast water velocities. In our model, costs increased with increasing water velocity, but they did not represent a large proportion of GEI. Puckett and Dill (1985) also found that prey capture costs are a relatively small proportion of the total energy budget for drift-feeding salmonids. This suggests that optimum velocity is more affected by prey capture probability than it is by costs. This may explain why drift-foraging models have been successful at predicting growth and habitat selection despite the assumption that prey capture costs are minimal (Fausch 1984, Hughes and Dill 1990, Hill and Grossman 1993, Nislow et al. 2000, Guensch et al. 2001, Hughes et al. 2003). Evidence that steelhead grow more quickly than do coho (Hartman 1965, Fraser 1969, Allee 1974, Bryant unpublished data), despite their selecting faster-velocity habitats, also contradicts the notion that coho exclude steelhead from mutually-preferred habitats. Faster growth in faster water is also seen for Atlantic salmon (Thorpe et al. 1992), for dominant, drift-feeding coho, that exclude subordinate conspecifics from faster water (Puckett and Dill 1985, Nielsen 1992).

Our results suggest that differences in energetic profitability between slow- and fast-velocity habitats cannot explain habitat segregation between juvenile coho and steelhead.

It is likely that the species have evolved differences that allow them to avoid overlap in resource use, and that segregation is largely selective, but we have little evidence to document this. Differences in size during their first growing season, and possibly differences in growth trajectories during their period of size overlap are two possibilities. Differential foraging abilities related to prey size or location might also facilitate coexistence during periods of prey limitations. These differences notwithstanding, there are likely times and places when interspecific competition between coho and steelhead is important. More intensive field surveys and experiments are needed to clearly document habitat selection by coho and steelhead. These surveys will need to include measures of habitat and prey availability as well as observations of habitat use, foraging, and agonistic behavior.

CONCLUSIONS

Predicted optimum foraging velocities for coho and steelhead differed by only 0.01 m · sec^{-1}, and modeled 10% and 25% increases in prey capture costs for coho reduced optimum velocity by 0 and 0.01 m · sec^{-1}, respectively. We conclude that velocity-dependent constraints on prey capture ability are more important than are prey capture costs in determining optimum velocities. Because these constraints are similar for coho and steelhead, we suggest that water velocity is not the primary niche axis upon which the species segregate stream habitat. Coupled with results from experiments showing that the relationship between prey capture rate and water depth differs little between coho and steelhead, we suggest that habitat segregation may be due factors other than short-term foraging considerations. We propose that these are largely selective mechanisms such as size-based habitat selection, differences in growth trajectories, or prey specialization, but we do not discount the possibility of interactive mechanisms.

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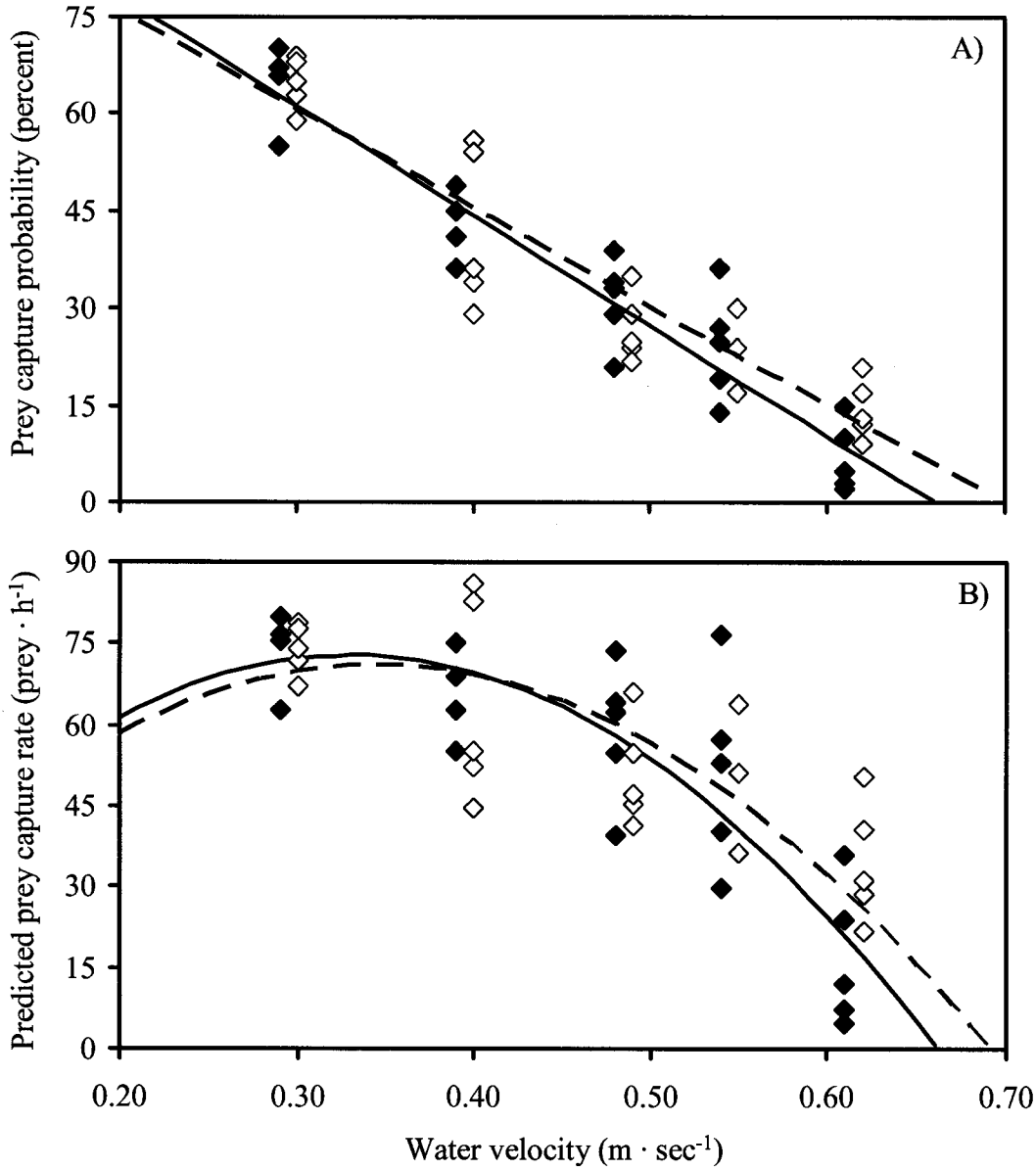

Figure 3.1. A) Prey capture probability vs. water velocity for coho (solid diamonds, line) and steelhead (open diamonds, dashed line). Regression equations and significance tests are found in Table 2.1. B) Predicted prey capture rate vs. water velocity for coho (solid diamonds and line) and steelhead (open diamonds, dashed line). Diamonds are the predicted prey capture rates for individual coho and steelhead (n = 5 for each species), and lines are predicted from the linear regressions from panel A. In both panels steelhead data points are offset +0.01 m · sec^{-1} for visual clarity.

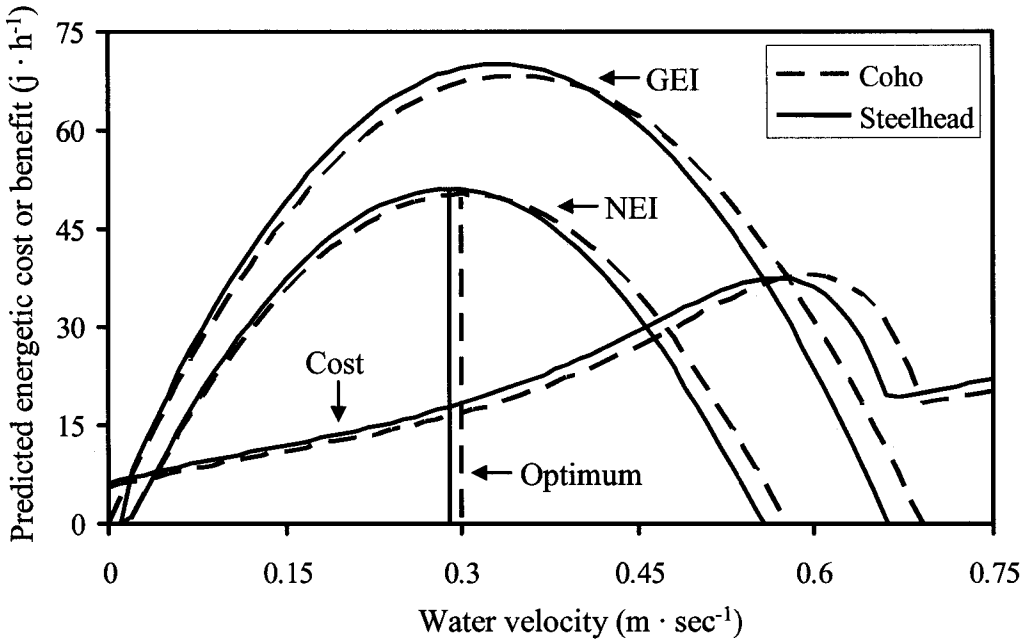

Figure 3.2. Estimated gross energy intake (GEI), net energy intake (NEI), and costs vs. water velocity for coho (solid lines) and steelhead (dashed lines). Vertical lines indicate optimum foraging velocity for coho (solid) and steelhead (dashed). The steep declines in the cost curves at fast velocities occur because as capture rates fall to zero, costs are only those of holding station at the focal point.

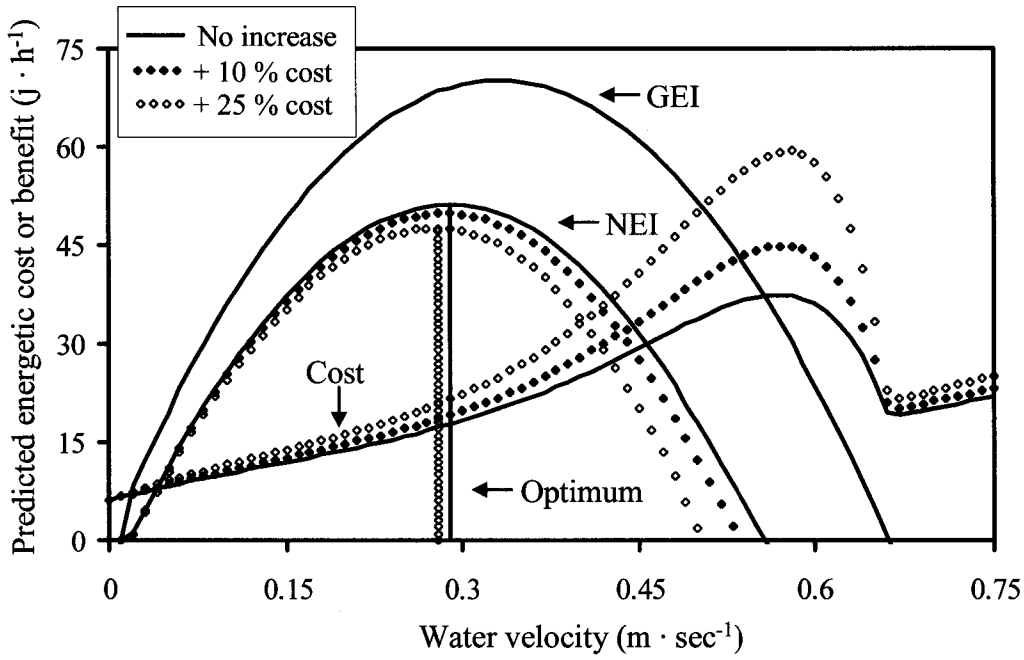

Figure 3.3. Estimated gross energy intake (GEI), net energy intake (NEI) and costs vs. water velocity for coho under three different cost scenarios relative to steelhead costs: 1) equal to steelhead (no increase, solid lines), 2) + 10% cost, solid diamonds, and 3) + 25% cost, open diamonds. Vertical lines indicate optimum foraging velocities (no increase and +10% costs are superimposed). The steep declines in the cost curves at fast velocities occur because as capture rates fall to zero, costs are only those of holding station at the focal point.

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GENERAL CONCLUSIONS

"The importance of theory (and experimentation) notwithstanding, the interpretation of niche and other ecological changes in nature must still rely heavily on informed professional judgment....So much must be done in so short a time to protect the remaining genetic diversity of these fishes that I cannot responsibly suspend judgments about trout biology and management in the hope that irrefutable data might one day be collected." Dr. Robert Behnke, Western Trout of North America

The results of my foraging experiments demonstrate that juvenile coho and steelhead possess a surprising degree of similarity in their foraging abilities. In addition, my NEI models predicted that there is little difference in optimal foraging velocities between the species, even assuming large increases in prey capture costs for coho. Taken together, these results suggest that habitat segregation between coho and steelhead is not based on differential foraging abilities. In weighing all of the available evidence, including my own observations of coho and steelhead in Southeast Alaska streams, and published studies of other pairs of sympatric stream salmonids (e.g. Everest and Chapman 1972), I think it is likely that habitat segregation between coho and steelhead is largely selective, although there is little evidence to document this. Differences in size during their first growing season, and differences in growth trajectories during their period of size overlap are two possible explanations for segregation. Differential foraging abilities related to prey size or location might also facilitate coexistence during periods of prey limitations. These differences notwithstanding, there are likely times and places when interspecific competition between coho and steelhead is important. More intensive field surveys and

experiments are needed to clearly document habitat selection by coho and steelhead. These surveys will need to include measures of habitat and prey availability as well as observations of habitat use, foraging, and agonistic behavior.

In theory, for similar species such as coho and steelhead to coexist their niches cannot completely overlap (Zaret and Rand 1971, Schoener 1974, Abrams 1983). During their first summer of growth, coho maintain a size advantage, and this alone may be enough to allow them to segregate stream habitat (e.g. Chinook and steelhead, Everest and Chapman 1972), even if size-matched fish have equal foraging abilities (e.g. Chapters One and Two). Studies that been done on age 0+ coho and steelhead have documented habitat segregation (Hartman 1965, Allee 1974, Bugert and Bjornn 1991, Young 2004), but they did not account for fish size or report behavior in natural streams. In streams where coho and steelhead have a size overlap during their second growth season, it is likely that temporal and spatial segregation in foraging occurs. Because the species appear to have similar foraging abilities, this segregation may be based more on long-term concerns such as growth trajectories, rather than on short-term energetic concerns. My limited field observations in Southeast Alaska suggest this is true, because I have documented two separate accounts of age I+ coho seeking cover under logs while age I+ steelhead and age 0+ coho actively foraged nearby. The temporal and spatial persistence of this pattern, however, is undocumented.

A discussion of the accepted ideas on Pacific salmon phylogeny, and how it may influence habitat segregation by coho and steelhead, is warranted here. Most researchers believe that the Pacific trout and salmon groups diverged from common ancestor by

around 5 million years ago. Fossil and molecular evidence points to the Pacific salmon group as having branched off the rainbow group (*Oncorhynchus mykiss* spp.) and this must have occurred before the subsequent separation and radiation of the semelparous Pacific salmon (Behnke 1992, Stearley and Smith 1993). *O. mykiss* and *O. kisutch* or their progenitors, therefore, have a long history of evolution, and potentially of coevolution, in fluvial environments. During this period the species would be expected to evolve differences that allow them to coexist, such as timing of life-history events, or differences in habitat preferences. Because both coho and steelhead usually spend at least a year in sympatry in streams, some of these differences are likely to involve this life phase.

It is tempting to speculate that steelhead, having come from the more ancestral lineage, colonized fluvial habitats before coho did. If so, they might have adapted to the most favorable habitats, such as fast-flowing water where energy, in the form of drifting invertebrates, was most available. When coho subsequently invaded, they were relegated to marginal habitats such as pools and backwaters, and they evolved strategies to cope with these, such as scrambling for prey, use of small streams, and large surplus reproduction (population sizes of coho are often an order of magnitude greater than those of steelhead (Fraser 1969, Allee 1974), a fact that first led Hartman (1965) to question how steelhead manage coexist). The fact that steelhead grow faster than do coho (Hartman 1956, Fraser 1969), and that coho grow faster in faster water (Puckett and Dill 1985, Nielsen 1992), supports the idea that these habitats are more favorable. Recent work by Rosenfeld et al. (2005) also shows that coho grow faster in habitats that include

riffles as well as pools. The long history of local extinction and recolonization by Pacific salmon due to glaciation, however, precludes such a simple model for coho and steelhead. The species must have carried their long-term adaptations to fluvial environments with them when they recolonized the Pacific Rim, and local populations later evolved specific strategies based on local environmental demands (e.g. spawning time, age of smolting).

Having evolved in a such highly-variable environment, both species, and salmonids in general, appear to have maintained considerable plasticity in their genomes (Hendry and Stearns 2004). This clearly extends to foraging abilities, because both coho and steelhead are able to forage in lacustrine as well as fluvial habitats. It may be that there are subtle differences in the species' relative abilities to forage on different prey types or sizes, or under different environmental conditions such as light intensity, that allow them to segregate habitat temporally or spatially or during times of limited resources. The later has been shown for two sympatric species of charr (Nakano 1999). Further experiments on the effects of prey size and type on coho and steelhead foraging are warranted, as are further observations of diurnal and seasonal patterns of habitat use.

In concluding that habitat segregation between coho and steelhead is largely selective, I think it is likely that there are also times when interspecific interactions are important. Intraspecific competition is widely documented in stream salmonids (Hearn 1987), although Fausch (1998) points out that in many cases direct experimental evidence is lacking. During periods of high population densities or low prey availability, coho and steelhead may directly compete for resources. Hartman's (1965) landmark laboratory

study of coho and steelhead remains the most detailed behavioral research. His finding, that habitat-specific differences in aggression facilitate segregation, is one likely explanation for how the species coexist during periods of resource limitation. Further experiments, however will be necessary to more clearly identify the underlying mechanisms responsible for habitat selection and segregation by coho and steelhead. These will need to include temporal and spatial aspects of habitat selection, and behavioral interactions between the species, particularly in natural streams where little research has been done. Forty years after Hartman (1965) first posed the question of how these two similar stream salmonids coexist, ecologists still have much to learn about habitat selection and segregation by juvenile coho and steelhead.

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